The Effects of Grazing by Parrotfishes (Family Scaridae) on Selected Shallow Hawaiian Marine Communities

by

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Abstract

THE EFFECTS OF GRAZING BY PARROTFISHES (FAMILY SCARIDAE) ON SELECTED SHALLOW HAWAIIAN MARINE COMMUNITIES

By Richard Eugene Brock

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This study has been conducted to: (1) assess the quantitative effects that rasping parrotfishes in a coral reef ecosystem have on the structure of benthic communities; (2) describe the standing crop of parrotfishes and (3) examine scarid recolonization patterns on a fish-depopulated patch reef.

Field studies were conducted at both Johnston Atoll and Kaneohe Bay, Oahu, Hawaii from 1975 through 1977. These studies suggest that there are two principal groups of Hawaiian parrotfishes, i.e., those with heavy dentition (*Scarus perspicillatus, S. sordidus* and *S. taeniurus*) that consume large quantities of calcium carbonate and probably utilize endolithic resources and those possessing relatively lightweight dentition (*Scarus dubius* and *Calotomus sandvicensis*) that appear to feed primarily on epilithic organisms. The latter species are not particularly abundant possibly due to competitive interactions with other herbivorous fishes (e.g., acanthurids) on Hawaiian reefs. Using an acid dissolution technique of extraction, the cryptobiota are estimated to range from 10 to 1400 g/m^2 (dry weight) and average about 50 g/m^2 in most Hawaiian reef systems. This potentially large food resource is systematically harvested by few other large reef species besides some parrotfishes and sea urchins.

Laboratory experiments conducted at the Hawaii Institute of Marine Biology in Kaneohe Bay using a flow-through seawater system suggests that parrotfish (*Scarus taeniurus*) at low density cause benthic community structure to proceed to macroalgal dominance. At intermediate density, (0.6 to 1.5 parrotfish/m^2 or 9 to 17 g wet weight/m^2) a diverse, high biomass community (to 400 g/m^2 dry weight) develops which may be enhanced by the presence of refuges. At *Scarus* densities greater than 1.9 fish (20 g wet weight per m^2) and in the absence of refuges, a benthic community of low diversity and biomass (3 to 8 g/m^2, dry weight) develops. Under high grazing pressure coralline algae are competitively superior as manifested through greater coverage.

Recruitment and growth of corals in the experimental situation correlates positively with increased grazing pressure and the presence of refuges ($P < 0.01$). These data suggest that parrotfishes may be important to the maintenance of the overall structure of coral reefs, thus acting as keystone species to other components of the benthic community. Parrotfish densities for optimum benthic community development in the laboratory are similar to those observed in some field situations (Kaneohe Bay, Oahu--1.1 fish or 10.8 g/m^2), and maximal growth of juveniles occurs at such densities.

Field experiments conducted at Johnston Atoll suggests that at normal field densities, parrotfishes may appreciably alter the benthic community structure in two dimensional (planar) systems. The addition of a third dimension (substratum depth) alleviates this negative impact. Coralline substratum samples exposed to average field grazing pressure tend to harbor a more diverse cryptofaunal community than

is present in substrata protected from grazers. The presence of a third dimension appears to give the epilithic and cryptobiotic components the protection from grazers necessary for survival.

Depopulation and recolonization studies conducted on an isolated Hawaiian patch reef suggests that the MacArthur-Wilson theory of island biogeography models the observed fish recolonization. The calculated wet biomass of fishes prior to depopulation was about 930 kg/ha which is in the range of other published studies. Fish community structure was dominated by planktivores (55% by weight) followed by carnivores (32%), herbivores (12%) and omnivores (2%). The large standing crop of planktivores was related to abundant plankton probably caused by local nutrient enrichment. Recolonization studies demonstrate that parrotfishes are one of the most successful groups to recolonize, suggesting that they are opportunistic in their habitat selection. A comparison of these data to those from the same reef 11 years earlier indicates that the structure of this community has been stable and has persisted in spite of local environmental change.

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CHAPTER 1

INTRODUCTORY REMARKS

Members of the parrotfish family (Scaridae) are one of the more common diurnally active fishes on Central Pacific and Caribbean coral reefs. Information other than taxonomic works concerning these fishes has been sparse. Ecologists studying tropical reef fish communities recently suggested that parrotfishes may be important in creating and maintaining the structure of benthic coral reef communities. Quantitative evidence of this role of parrotfishes has been lacking. Management of a species is necessarily based not only on its biology but also on its ecological role in the community. This study was undertaken to describe and quantify the ecological effects of parrotfish on reef systems particularly in Hawaii. Such an approach is important to the understanding and management of the entire coral reef ecosystem.

Many parrotfish species have been described as herbivores that actively rasp the substratum in their feeding. Herbivorous fishes have been classified in various ways by different authors according to their methods of feeding. Bakus (1967) considered fishes that feed by rasping as synonymous with those that graze but differentiated them from browsers, fishes which consume benthic algae but do not scour the substratum. Jones (1968*a*) in his study of the feeding relationships of Hawaiian Acanthuridae (surgeonfishes) characterized the benthic feeding species as either browsers or grazers. He described browsers as "strict herbivores that bite and tear off bits of

multicellular benthic algae generally without ingesting any of the inorganic substratum," and grazers as fishes that pick up large quantities of the substratum during feeding "irrespective of whether the material is rasped away from rock or picked up as loose sand." None of the surgeonfishes in Jone's study actually rasped the substratum in Hawaiian or Johnston waters; four species of *Acanthurus* ingested sand and two species of *Ctenochaetus* fed on fine detritus blanketing hard substrata.

In this study, I define browsers as did Bakus (1967) and Jones (1968*a*), grazers as herbivorous species ingesting loose bottom particles (sand and fine detritus), and raspers as species that actively scrape solid substrata while feeding. Parrotfishes are rasping herbivores that are common on coral reefs.

Literature quantitatively describing the effects of tropical marine browsing, grazing or rasping fishes is sparse. Many authors have suggested that grazing and rasping species in tropical reef systems affect the benthic communities in which they feed, but their data were based either on rough field observations or poorly controlled field experiments (Bakus 1964).

In general, a greater algal standing crop results when subtidal substratum is protected by cages from herbivorous fishes (Stephenson and Searles 1960, Randall 1961*a*). Stephenson and Searles (1960) noted that algae protected from herbivorous fishes not only became thicker, but also more unstable, breaking off and creating bare patches which were colonized by the same or other algal species.

Bakus (1964) at Fanning Island (Line Islands) noted that when exposed, the normally cryptic sessile invertebrate species are rasped

away by grazing fishes. Bakus (1966, 1969, 1972) proposed that this tropical coral reef cryptofauna evolved its secretive habits in response to predation by herbivorous fishes. Bakus (1972) suggested that the activities of rasping fishes may prevent species dominance and create patchiness in these coral reef communities. Dart (1972) working in the Red Sea concluded that colonization of corals on hard substrata in the reef crest zone is facilitated by the grazing of algae by echinoids and fishes. Earle (1972) showed that on a Caribbean reef an inverse relationship existed between the number of herbivorous fishes and the standing crop of macroalgae. John and Poole (1973) reported that in the Gulf of Guinea larger fleshy algae were replaced by more herbivore-tolerant species such as corallines and encrusting forms where grazing pressure was high.

Studies of a more quantitative nature were undertaken by Vine (1974) and Birkeland (1977). Vine found that territories defended by pomacentrids had greater standing crops of green filamentous algae than did adjacent reef areas exposed to herbivorous fishes in the Red Sea. He showed experimentally that the increase of foliaceous algae in these territories obstructed the settlement and growth of benthic invertebrates (e.g., tube worms (*Spirorbis* spp.)) and hindered the growth of coralline algae which cement the substratum. Vine concluded that herbivorous fishes are important to the maintenance of the benthic community. In a study of coral recruitment under varying environmental conditions, Birkeland (1977) demonstrated experimentally that herbivorous fishes enhance the survival of coral recruits on settlement plates in the Caribbean Sea.

In summary, these studies show that herbivorous fishes may

reduce the standing crop of algae, increase algal diversity, and feed on benthic invertebrates if they are exposed. Recent experimental work has brought attention to the role played by these herbivorous species in providing space for settlement, growth, and maintenance of benthic invertebrate species. These studies have not attempted to discern the differential effects of grazing and rasping on the benthic biota by various herbivorous fish species. Information on the species composition of these herbivores on many coral reefs is sparse.

Analysis of gut contents is an important method for determining which fishes are herbivorous. Analyses of tropical marine herbivorous species have been made from geographically scattered areas, but many of the species range from the Red Sea across the Indo-Pacific to Hawaii. These studies include work of Suyehiro (1942) in Japan, Al-Hussaini (1947) in the Red Sea, Dawson et al. (1955) in the Line Islands, Hiatt and Strasburg (1960) in the Marshall Islands, Stephenson and Searles (1960) in Australia, Randall (1961*b*), Jones (1968) and Hobson (1974) in Hawaii, Randall (1967) in the West Indies, and Vivien (1973) in Madagascar.

Hawaiian obligate herbivores are found in the families Kyphosidae, Acanthuridae and Scaridae (Hobson 1974, Randall 1974). There are seven recognized Hawaiian species in the family Scaridae (*Calotomus sandvicensis, C. japonicus, Scarops rubroviolaceus, Scarus dubius, S. perspicillatus, S. sordidus,* and *S. taeniurus* (see also Schultz 1958)). The following species of Acanthuridae are herbivorous browsers in Hawaii: *Acanthurus triostegus sandvicensis, A. guttatus, A. achilles, A. glaucopareius, A. leucopareius, A. nigrofuscus, A. nigroris, A. olivaceus, A. mata, A. dussumieri,*

A. xanthopterus, Ctenochaetus strigosus, C. hawaiianesis, Zebrasoma flavescens, Z. velifrum, Naso literatus, N. brevirostris and *N. unicornis* (Jones 1968, Randall 1961*b*). In the family Kyphosidae there is one inshore species (*Kyphosus cinerascens*) that is a browsing herbivore (Gosline and Brock 1960). Hobson (1974) noted two other strictly herbivorous browsers, the angelfish *Centropyge potteri* and the blenny *Cirripectus variolosus*. Both species are relatively uncommon. Many carnivores will ingest algae, coral and sand incidental to their prey (Randall 1967). These fishes are not included with the omnivores. Omnivorous species in Hawaii include members of the families Chaetodontidae, Pomacentridae, Labridae, Balistidae, Monacanthidae and Canthigasteridae (Reese 1973, Hobson 1974, Randall 1974, Hiatt and Strasburg 1960).

The number of strictly herbivorous reef fish species (38) in Hawaii appears small relative to the approximate 450 species of inshore fishes known from the islands. However, the above survey of the literature has provided some insight into the potential importance of some of these fishes in either modifying or maintaining their coral reef habitat. The present research has been undertaken to increase the understanding of the influence of these fishes on coral reef community structure and succession by providing quantitative answers to the following questions:

1. What influence do herbivorous fishes have on benthic community structure and species diversity?
2. Are "keystone species" (sensu Paine 1969) present, and if so, how do they affect benthic communities?
3. What proportion of the standing crops of algae and benthic

invertebrates (both epi- and infaunal) are utilized as food by the major rasping fish species?

These questions will be restricted to herbivorous fishes that feed by actively rasping the substratum. These fishes are primarily in the parrotfish family Scaridae whose members comprise one of the more ubiquitous groups of fishes on modern coral reefs. Two environments are employed in this study; one nutrient enriched (Kaneohe Bay, Oahu) and the other a pristine coral reef (at Johnson Atoll), both in the Hawaiian faunal region.

CHAPTER 2

HAWAIIAN REEF SYSTEMS AND STUDY SITES

Introduction

The reefs of the high Hawaiian Islands differ in structure and composition from those found in other Central Pacific localities; thus a summary of their general characteristics is given below. The Hawaiian Archipelago is 2575 km long, oriented in a northwest-southeast direction. The northwestern half of the chain is comprised of low coral atolls and flat islands; those islands to the southeast are geographically younger and are high oceanic islands. The older high islands, e.g., Kauai, Oahu, and Molokai have more extensive reef flats than do the younger islands of Maui and Hawaii. Along the beaches of the high islands benches are an important shoreline component that make up about one half of the coastline. These bench systems on the island of Oahu have been described in detail by Wentworth (1938, 1939). McLean (1974) has studied bioerosion on benches, and Kohn (1959) has discussed components of the fauna found on selected Oahu benches.

Fringing reefs are the most common type of Hawaiian reef and according to Moberly and Chamberlain (1964) they occur in three forms which grade into one another. The three forms are (1) the wide and usually shallow (water depth less than 4 m) reefs normally off windward coasts, (2) reefs with a greater width than windward reefs and less depth (less than 1 m) usually along protected (leeward)

coasts and (3) the deeper, more irregular reefs of northern and some leeward coasts. The reefs along the windward coastlines of the older high islands (particularly Oahu and Kauai) are often dissected by channels to a depth of 20-30 m opposite stream mouths. The only barrier reef in the Hawaiian Islands with a relatively deep lagoon behind it fronts Kaneohe Bay, Oahu, one of the two study areas.

The substratum of Hawaiian fringing reefs is characteristically dominated by sand and rubble; corals and coralline algae are usually seen in the outer areas of the reef platform and on the seaward reef slope. Generally, where there is vertical relief or habitat heterogeneity, a greater diversity of invertebrate species and fishes will be encountered. This often occurs seaward of the algal ridge on most fringing reefs. Around the geologically younger islands of Hawaii and Maui, reef development is not as advanced; there, lava rock and corals provide a series of diverse habitats. These coral communities and the colonization of new lava flows have been studied by Grigg and Maragos (1974).

On exposed coasts, surf is a major factor regulating the distribution of invertebrate and fish species to a depth of at least 20 m in depth (Gosline 1965). General discussions of Hawaiian coral reefs may be found in Agassiz (1889), McCaughey (1918) and Moberly et al. (1963) who have mapped the distribution of corals, sand, limestone and described the general underwater topography at selected localities around six of the islands.

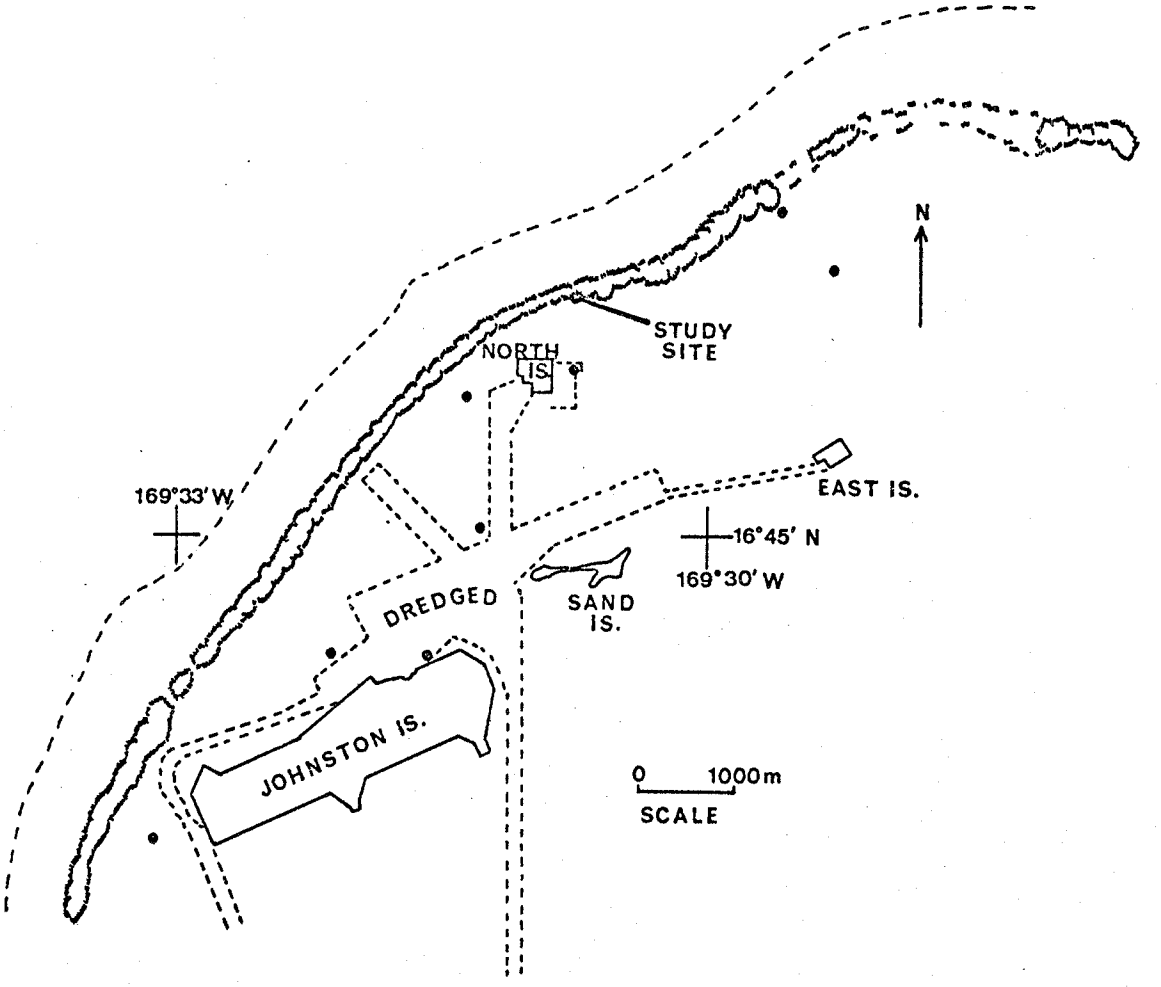
Johnston Atoll

Johnston Atoll consists of a 22 by 11 km coral reef platform with four small islets located at approximately 16°45'N, 169°31'W. The closest land mass to Johnston is about 725 km to the northeast (French Frigate Shoals in the Hawaiian Archipelago). Geological features of Johnston have been discussed in detail by Emery (1956). Basically, the coral-algal platform is shallowest towards the northeast (windward) edge and gently slopes off towards the southwest until the 29 m contour is met; from that point the depth rapidly increases. The windward aspect of the main reef presents a near-vertical face into deep water. Two of the islets in the lagoon are man-made (Amerson and Shelton 1976) and the marine habitats adjacent to all four islets have been subjected to sporadic dredging since 1940. Unlike most atolls the natural islets lie from 0.8 to 2.4 km inside the lagoon from the crest of the windward reef (see Figure 1). The geomorphology of Johnston has been described by Ashmore (1973) and a summary of the history and climate is given in Amerson and Shelton (1976).

Johnston Atoll is situated in the northeast tradewind belt and is bathed by the North Equatorial current. Kopenski and Wennekens (1966) have studied the circulation in and around the atoll. In general the flow of water over the platform is in a westerly direction but is modified by the tides, particularly during the summer months.

Biological collections made over the years by Edmondson et al. (1925), Fowler and Ball (1925), Wells (1954), Gosline (1955), Brock et al. (1965), Brock et al. (1966), Buggeln and Tsuda (1966), Brock

Figure 1. The northern part of Johnston Atoll showing the location of the major study site and eight other study areas which are shown by darkened circles. Islets are outlined by solid lines, dredged areas within the lagoon by dashed lines. The 200 m depth contour is shown seaward of the windward reef as a dashed line (map redrawn from Amerson and Shelton 1976).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STUDY SITE
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169°33' W
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16°45' N
169°30' W
SAND IS.
DREDGED
JOHNSTON IS.
0 1000m
SCALE

(1972), Brock (1973), and Bailey-Brock (1976) suggest that the marine fauna is primarily Hawaiian complemented by a few Central Pacific elements. However, the dominant corals at Johnston belong to the genus *Acropora*. The genus is near-absent from the remainder of the Hawaiian faunal region and the *Acropora* at Johnston provides habitats that greatly differ from those seen around the Hawaiian Islands. Apart from the dredged portions (see Figure 1), marine areas of Johnston Atoll probably have undergone little disturbance by man and hence may be considered a pristine reef system.

Unlike most atolls, Johnston has a marginal reef only on one side (approximately paralleling the northeast tradewinds) and it also lacks a deep lagoon. The shallow lagoon has extensive coral growth. Wells (1954) recognized that the lagoon corals are dominated by the large plate-like *Acropora hyacinthus* and Emery (1956) noted the abundance of massive coral mounds often covered by *Montipora* spp. in this area. Brock et al. (1965) in their study of nine major habitats in the Johnston lagoon estimated that the average coral coverage for the non-dredged areas is roughly 58 percent. Smith and Harrison (1977) suggested that the Johnston lagoon may be an optimum environment for coral growth by being relatively shallow and having appreciable water motion but protected from excessive wave action.

The primary study site selected at Johnston is situated just to the lee of the shallow reef northeast of North Island in the rubble-talus zone of Emery (1956). The substratum of the zone is made up of talus and coral shingle that slopes away lagoonward to an area of high coral coverage dominated by *Acropora hyacinthus*. The reef crest (or algal ridge) and the seaward slope are composed almost

entirely of coralline algae and the few corals found in the seaward region are species that can take on low crustose growth forms (*Pocillopora, Montipora* and *Porites*) or ahermatypic corals that can live in crevices, e.g., *Distichopora* (Wells 1954). The lack of corals on the algal ridge or seaward is probably due to high water motion caused by incoming waves particularly during the winter months. The talus slope or rubble zone just inside of the algal ridge is continuous along most of the length of the windward reef (see Figure 1) and varies in width from 20 m to over 100 m. It probably represents one of the few consistently open areas free of much coral coverage and is accessible for study due to its protected location behind the algal ridge. Between the algal ridge and the talus slope is the *Acropora humilis* zone of Wells (1954). This zone is patchy depending on bottom topography and hence coral coverage is quite variable. Coral species commonly occurring include *Acropora humilis, A. retusa, Montipora, Pocillopora, Porites lobata* and *Millepora*; most corals in this area have prostrate growth forms probably in response to water motion.

Where coral coverage is high, areas open for algal recruitment and grazing by fishes are fewer. Coral structures provide cover for these fishes but open space is essential to their feeding (Smith and Tyler 1972, Smith 1978). In general more herbivorous fishes occur in areas of low coral coverage at Johnston Atoll. Fourteen 4 × 20 m visual transects were conducted in different habitats in the Johnston lagoon. Seven areas were relatively low in coral coverage and seven habitats had high coral coverage. Thirty-eight percent of the species and 72% of the individual fishes censused in the low coral coverage

areas were strict herbivores; in the high coverage habitats 34% of the species and 58% of the individuals were herbivores (estimates probably only accurate to within 5% of the true values due to errors inherent in the visual census technique). However, in the latter areas most of the grazers and raspers were juveniles, but in the low coverage habitats, herbivorous fishes of all sizes were censused.

The greater abundance of rasping fishes and continuous open substratum for algal growth, epi- and infaunal recruitment, and appreciable water motion sets the rubble-talus zone apart from many other reef areas at Johnston Atoll. These attributes along with its accessibility were reasons for choosing this area for experiments that were conducted to examine the effects of herbivorous fishes on coral reef community structure at Johnston Atoll.

Kaneohe Bay

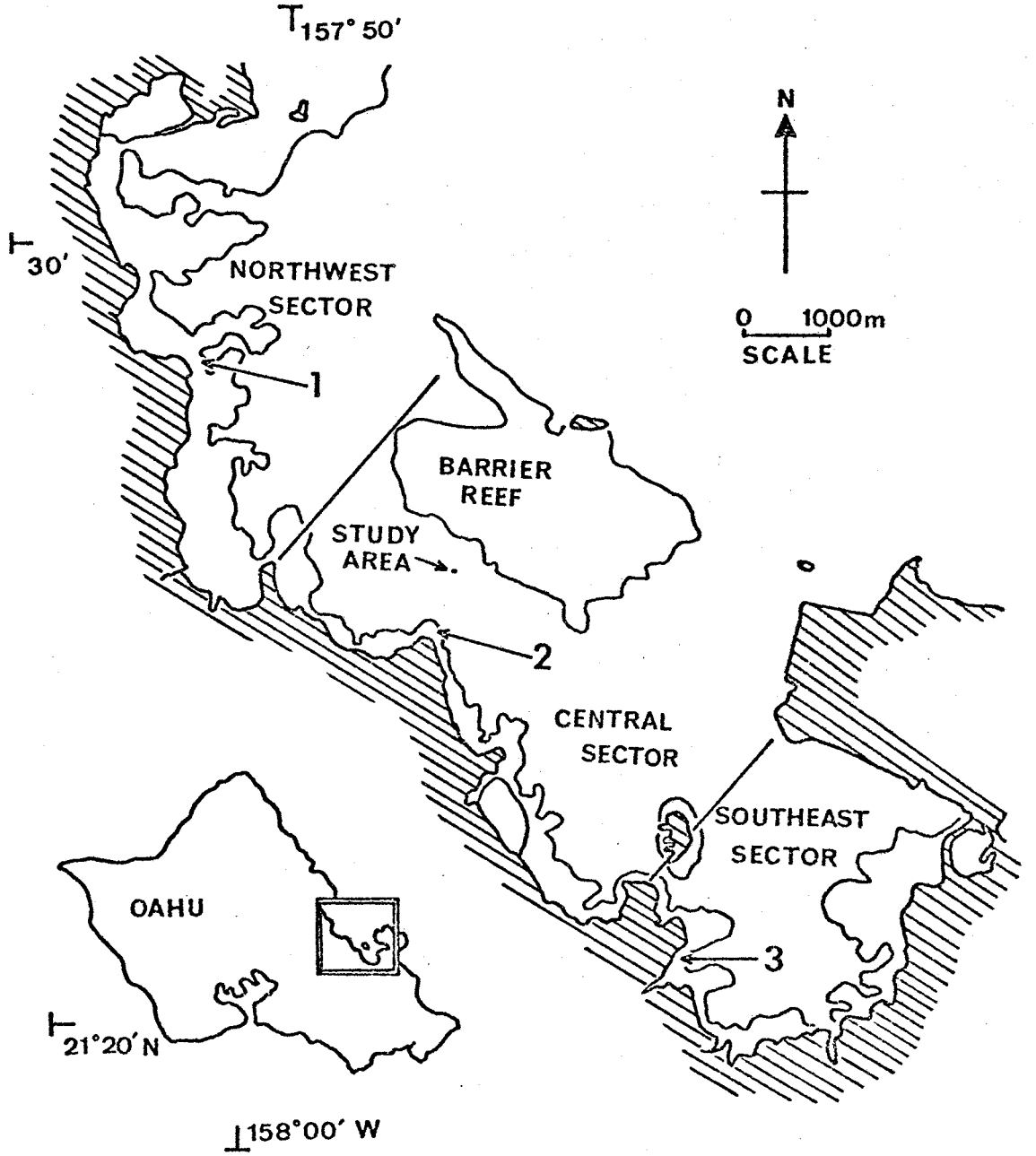
Kaneohe Bay on the windward side of Oahu is the largest sheltered body of water in the high Hawaiian Islands that is fronted by a barrier reef and has a lagoon with patch reefs within. Years ago the bay was well known for its luxuriant coral gardens particularly in the southern portion (MacCaughey 1918, Edmondson 1928). During the 1940's dredging operations were undertaken in the bay to create ship channels and seaplane runways. Literature on the bay includes a historical account by Devaney et al. (1976), current systems by Bathen (1968), bathymetry by Roy (1970), and an annotated bibliography by Gordon and Helfrich (1970).

In recent years Kaneohe Bay has become an environmental issue (Banner 1974, S.V. Smith 1977). Urbanization of the Kaneohe Bay

watershed has brought two major stresses to the bay. Land development and stream channelization have caused runoff of sediment-laden water during heavy rainfall. A municipal sewage treatment plant began dumping secondarily treated sewage into the southern portion of the bay in 1963. These perturbations and the current regime divide the bay into three major regions (Figure 2). Of the three, the southeastern sector is most altered by man. It may be characterized by a large sewage influx and stream flow into an area having poor circulation and exchange with the open ocean. The central sector containing the major study site receives little runoff or sewage and is fronted by the shallow barrier reef. The northwestern sector has relatively good oceanic exchange due to the 1 m greater depth of the barrier reef in this section. The watershed of this region is agricultural rather than urban with sediment-laden stream runoff being the major terrestrial influence on the area.

S.V. Smith (1977) in his analysis of freshwater and nutrient budgets of Kaneohe Bay noted that 90% of the freshwater delivered annually to the bay occurs between November and April. The northwest sector receives 57% of the freshwater, the central area gets 3% and the southeast region, 40% of the input. In the nutrient budget, sewage contributes about 70% of the inorganic nitrogen and 83% of the inorganic phosphorus entering the bay from terrestrial sources. Nutrient loading varies greatly from one sector to another. However S.V. Smith (1977) remarked that differences in nutrient concentration among sectors is small. He attributed this lack of difference in nutrient levels to high biological activity particularly in the southern sector. The sewage input into the southern sector was terminated in

Figure 2. Map of Kaneohe Bay, Oahu, Hawaii showing the location of the major study site (experimental reef discussed in Chapter 8) and three other study areas (numbered 1, 2, and 3) located in each sector (Northwestern, Central and Southeastern). Reef areas are outlined with solid lines and land areas are crosshatched. The Hawaii Institute of Marine Biology is on Coconut Island in the southeastern sector of the bay.


157° 50'
30'
NORTHWEST
SECTOR
1
BARRIER
REEF
STUDY
AREA
2
CENTRAL
SECTOR
SOUTHEAST
SECTOR
3
OAHU
21°20' N
158°00' W
N
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SCALE

December 1977 in compliance with federal water quality standards.

Biologically, Kaneohe Bay is one of the better known coastal areas in the Hawaiian Islands. Biological work prior to 1970 was presented as a bibliography in Gordon and Helfrich (1970). Smith et al. (1973) described many of the biological components of the bay. Johannes (1975), S.V. Smith (1977) and Brock and Brock (1977) discussed responses of the benthic communities to sewage, silting and freshwater influences.

In general the benthic communities of the southeastern sector are dominated on the reef tops and slopes by suspension-, filter-, and deposit-feeding forms. Very little live coral is found in this sector. Benthic biomass is high, averaging 521 g/m^2 dry weight (Brock and Brock 1977). Most fish species in this region are either detritivores or planktivores. Moderate coral coverage along the slopes and crests of reefs characterize the central region of the bay where infaunal biomass is relatively low ($\bar{x}$ = 151 g/m^2 dry weight; Brock and Brock 1977). Fish species in this area include many herbivores (parrotfishes) as well as omnivores and carnivores. Planktivorous fishes however, are the most abundant. Both the central and northwestern sectors have large standing crops of the alga *Dictyosphaeria cavenosa* along the reef slopes. This alga may be locally abundant and on some reefs covers 100% of the substratum. Banner and Bailey (1970) reported heavy concentrations of this alga in the northern part of the southeastern sector in 1969-70. It has essentially disappeared from that part of the bay.

The inshore reef slopes and crests of the northwestern sector are characterized by benthos that can survive under silty conditions.

Corals are patchy. Infaunal species are relatively abundant; Brock and Brock (1977) found an average biomass of 277 g/m^2 (dry weight). Inshore fishes are mostly juveniles. The lagoon floor makes up the largest area of a single substratum type in Kaneohe Bay. It is composed of fine sediments (Roy 1970, Smith et al. 1973) and is located among the fringing, patch and barrier reefs. Organisms present in lagoonal muds include detritus-feeding crabs, burrowing shrimps and a few deposit-feeding polychaetes. The infaunal biomass and the species composition of the lagoon floor habitat is similar for all sectors of the bay; the biomass averages between 3 and 5 g/m^2 in dry weight.

Studies on grazing fishes have been carried out in many parts of the bay; three of these sites coincided with a continuing study and one was located in each of the three sectors (Figure 2). As noted above, the major study site was located on a patch reef in the central sector and is discussed in Chapter 8.

CHAPTER 3

FIELD METHODS

This chapter is concerned with methods used in the field surveys. Techniques used in laboratory experiments and analyses are given in other chapters.

Johnston Atoll

The location of the study site at Johnston (Figure 1) is in the rubble-talus zone between the algal ridge of the windward reef and the *Acropora hyacinthus* zone of Wells (1954). The rubble zone in this area is roughly 70 m in width and extends the length of the shallow windward reef. A 10 × 10 m area located in 2 to 3 m of water was chosen as being representative of the rubble zone for fish and invertebrate censusing. This permanent quadrat was marked at each corner by a metal stake.

Three experimental cages were set along the deeper (lagoonward) side of this study area. These cages were put out to study the effects of rasping by fishes and sea urchins on benthic communities. Cages measuring 61 × 61 × 15 cm were equipped with adjacent "roofs" (61 × 61 cm) and accessory cages (15 × 15 × 5 cm) to hold settlement plates. The "roof" held 15 cm off of the bottom served as a control for impinging light and allowed the herbivores to feed under it. The cages were constructed of heavy duty galvanized wire screening with 2.5 × 2.5 cm mesh. After construction the cages were painted with an epoxy paint to retard rusting. The three cages were

first put out on 27 May 1975 and replaced during each subsequent visit (17 August 1975, 14 October 1975, and 24 April 1976). The cages were held in place by steel reinforcing stakes, 1.3 cm in diameter, driven about 75 cm into the substratum at the corners of the cages and roofs. Nylon cord was used to hold the cages in place.

Sampling commenced by stringing a piece of cord around the stakes to delimit a 10 × 10 m census area. Because fishes did not shy away from the diver, they could be censused immediately. This was accomplished by using a method modified from Brock (1954) whereby all fishes seen within the prescribed area were tallied by a SCUBA diver using a slate inscribed with the names of common species. Larger and easily recognizable fishes were censused from a single point in the center of the study area by moving in a 360° arc; smaller species were tallied by swimming over the entire area. Approximately 15 minutes were spent censusing fishes during each sampling. The validity of the visual censusing method is discussed in Chapter 8.

A tally of the sea urchin population within the 10 × 10 m study area followed the fish censusing. Numbers and species of these echinoids were listed and their average test sizes were estimated.

Substratum sampling for epi- and infaunal community composition and biomass was done by collecting pieces of coral rock adjacent to each cage and from under each roof and placing each into a labeled plastic bag. These samples were all approximately 10 × 10 cm in exposed surface area. Samples taken adjacent to each cage and from under each roof served as controls; ungrazed substratum from within each cage was taken by loosening the cage holdfasts and removing a piece of material. All samples were held in separate bags, and on

return to the shore, were preserved in 10% formalin. In all cases the removal of a piece of substratum caused a large number of wrasses and parrotfishes to gather about to graze on any newly exposed surface. Therefore, cages had to be replaced quickly. Only one cage was loosened, sampled and replaced at a time to minimize such predation.

Settlement plates (10 × 10 cm ceramic tiles) were held in place by nylon cord through two holes drilled along one side of the tile. Exposed tiles were collected, put into labeled plastic bags and later preserved in 10% formalin. Tiles removed were replaced immediately with clean ones.

Substratum relief in the rubble and talus zone was measured along a 5 m transect to obtain an estimate of surface area. Also, adjacent to the 10 × 10 m quadrat the rubble and all organisms were removed from a 0.25 m^2 area to a depth of 10 cm. This rubble was used in surface area determinations in the laboratory by the aluminum foil method discussed below.

In April, 1976 a *Porites lobata* coral head (28 cm in diameter) was removed from the vicinity of the study area for an analysis of the growth bands which may be used in determining the recent environmental history of the area (Buddemeier 1974). In addition, a transect for coral cover and community composition was conducted from the reef crest (algal ridge) down through the study site. This was accomplished by using a 1 m^2 quadrat subdivided into 10 × 10 cm grid. The quadrat was placed end over end for 90 m (bisecting the study area). Data were recorded as the percent coverage of each species present in each quadrat.

Besides the major study site, eight other areas (Figure 1) were surveyed in April 1976. These surveys included estimates of coral cover and diversity, censuses of fishes and macro-invertebrates, and samplings of hard bottom material for infaunal community composition. At some of these stations, as well as at the study site, relative water motion was estimated.

Herbivorous fish were collected for gut content analysis more than 400 m northeast of the study site in the rubble-talus zone during each visit to Johnston. Fishes were collected principally by spear and also with 5% rotenone. All specimens were labeled, injected and preserved in 10% formalin. The author has conducted research at Johnston Atoll intermittently since 1970. During this period, animals not previously recorded from Johnston Atoll were collected from various habitats to obtain a better understanding of the distribution of the Hawaiian fauna. Specimens were deposited in the B.P. Bishop Museum in Honolulu.

Kaneohe Bay

Four habitats were selected in Kaneohe Bay, Oahu as study sites for various aspects of this research (Figure 2). Sampling stations were set up in each of the three major zones of the bay (southeastern, central and northwestern sectors) by personnel studying the effects of termination of sewage discharge in the bay (under U.S. Environmental Protection Agency Contract No. R803983). The same stations were used in the present study, considering them to be representative of each sector. Data were taken bimonthly. Samples included 4 × 20 m fish and macro-invertebrate visual census transects

and substratum material for epi- and infaunal community structure and biomass. Some of these data have been used in the present study for comparative purposes. Herbivorous fishes were collected from various parts of the bay for gut content analysis.

A fourth study site was located on an isolated patch reef in the central sector. Fishes residing on the reef were removed by rotenone to determine the community structure and recolonization patterns particularly with regard to the parrotfishes. The methods used on this reef are discussed in detail in Chapter 8.

Substratum relief and surface area in marine communities is important; greater relief provides organisms with a more diverse series of habitats and this structural diversity presents a greater surface area over which more energy may flow. The quantification of substratum relief in marine communities is not a simple task. Kohn (1967) used a subjective rating of habitat complexity, Risk (1972) employed a 1-m chain draped over the bottom along a measured linear distance. He assumed that the actual surface area was proportional to the square of the sum of the lengths of the draped series of chain. Dahl (1972) estimated reef surface area by use of simple geometric approximations (plates, cylinders, cones) at appropriate scales and expressed his results as a surface index. The surface index is defined as the ratio of the actual surface to that of a plane with the same boundaries.

Marsh (1970) developed a method estimating calcareous algal surface area by first determining the weight per unit area of aluminum foil stock, then weighing the amount of foil it took to just cover the surface of the algal sample. This method is useful for small objects and surfaces lacking much complexity. Johannes et al. (1970) used

this method to determine the surface area of corals.

At both the Johnston and the Kaneohe study sites an attempt was made to use the chain method. The large amount of water moving in over the reef at Johnston made the measurement of surface area in the rubble zone difficult. Therefore, rubble inside a 0.25 m^2 area was photographed, removed, and transported to Honolulu for further study. The upper or exposed surfaces of this rubble was distinguishable by the microalgal community present. The exposed portions of this rubble were measured by the aluminum foil method.

The "clod card" method (Doty 1971) was used to assess relative water motion. This technique relies on the dissolution of plaster of Paris cubes cemented on to plastic cards ("clod cards") set out in the field. The dissolution of these calcium sulfate cubes is enhanced by water movement. "Clod cards" were initially weighed dry, set out in the field generally for 24 hours, collected, dried, and reweighed. Calibration of cards is necessary and is done by allowing dissolution of a series of clod cards to occur in still water. A calibration value (k) is determined by the equation

$$k = Mc \frac{(te)}{(tc)}$$

where Mc is the mass lost for the calibration period (tc) and te is the field exposure period. The calibration value is divided into the weight lost by each clod card during its time of immersion in the field so that a diffusion factor (DF) is obtained. The diffusion factor is a measure of the dissolution enhanced by water movement.

CHAPTER 4

ENVIRONMENTAL FEATURES OF THE JOHNSTON ATOLL STUDY SITE

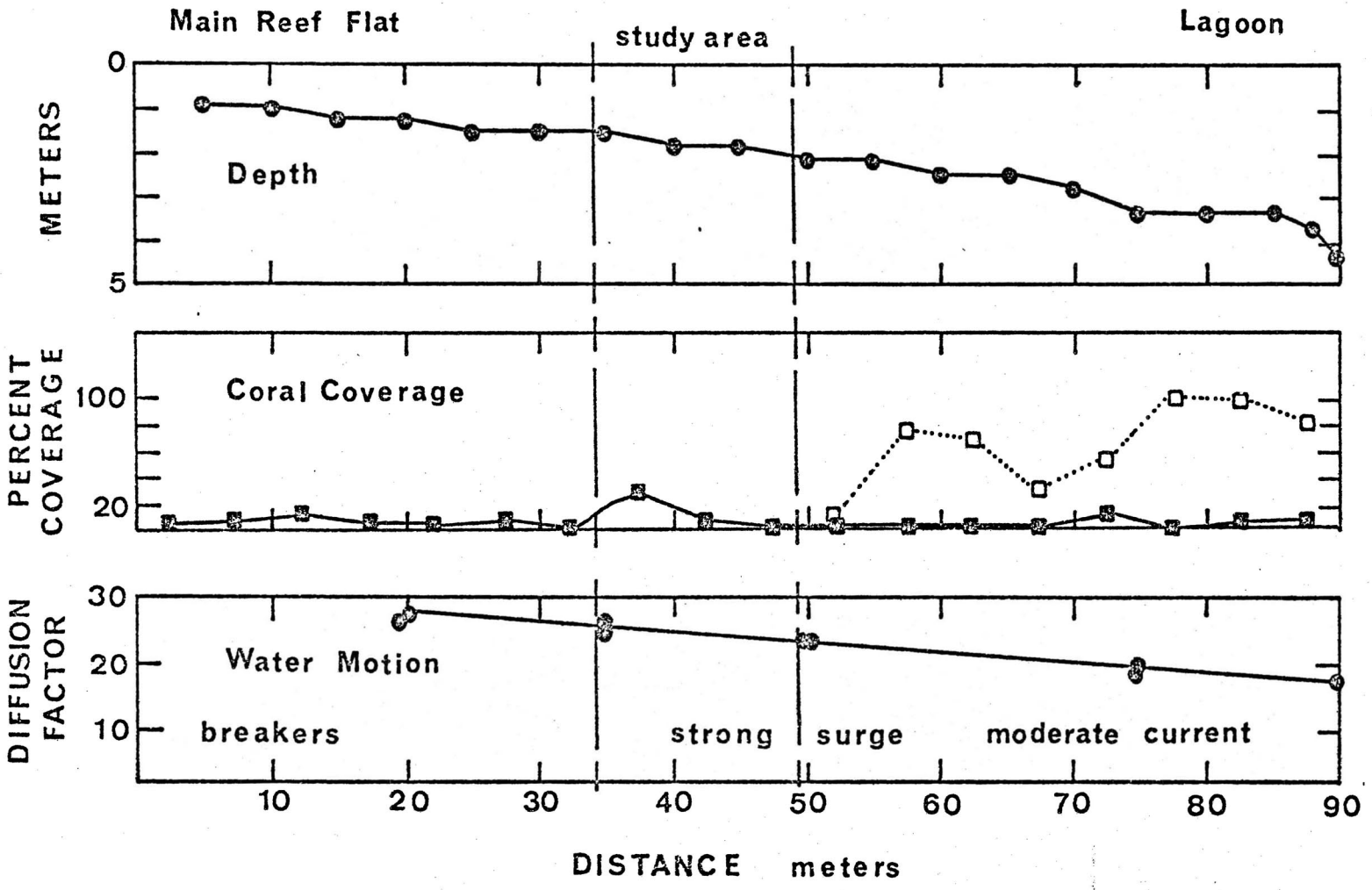
The windward fore-reef and crest of the algal ridge dissipate most of the energy of incoming waves. From the crest of the algal ridge, water depth increases steadily lagoonward and abruptly seaward. The depth profile on the lagoon side increases from 5 to 15 cm at the crest to over 4.5 m in the *Acropora hyacinthus* zone about 80 m lagoonward of the reef crest, resulting in a loss of wave energy. This depth gradient is plotted in Figure 3-A beginning about 8 m lagoonward of the shallowest part of the reef crest, crossing the study site and continuing for 35 m into the *Acropora hyacinthus* zone. Relative water motion was measured over a 24 hour period on 24-25 April 1976 through an area bisecting the study area. Tradewinds were normal (16-29 km per hour, National Weather Service) and surf height breaking on the windward reef was approximately 1 m. The water velocity calculations described in Chapter 3, are plotted in Figure 3-C against increasing water depth moving lagoonward. Linear regression of the expected diffusion factor $\hat{Y}$, on water depth, x , yields the equation, $\hat{Y} = 30.37 - 3.34\,x$. The coefficient of determination ($r^2 = 0.74$) is significant ($P < 0.001$). The coefficients of the equation hold only for a limited range in surf and wind conditions. The windward reef is exposed to the full impact of winter and storm generated surf coming from a northerly direction. The author has witnessed waves estimated to be 3 to 4 m high breaking on the reef;

at such times a swimmer is not able to get within 100 m of the study site because of the large volume of water crossing the reef. Obviously the diffusion factor equation given above is applicable only to a narrow range of wind and surf conditions.

The strong water motion characteristic of the Johnston Atoll study site is probably responsible for the relatively large amount of coral-free substratum present in the rubble zone. This open space is attributable to substratum instability. The dissipation of wave energy in the rubble zone causes substratum turnover and abrasion. Benthic species inhabiting such an environment possess heavy shells (e.g., some gastropod mollusks and xanthid crabs) or rapid colonization and high turnover characteristics. Corals are not particularly abrasion resistant nor are they species with rapid growth. But where wave energy has dissipated to a point where the substratum becomes stable, corals dominate the benthic community. As shown in Figure 3-B, coral coverage is low from the algal ridge, across the rubble zone until the *Acropora hyacinthus* zone is encountered. *Acropora hyacinthus* has an overlapping growth morphology allowing coverage values to exceed 100% if all coral surfaces are considered. Coral coverage is defined as the percentage of the substratum in a given area covered by live corals as viewed from a vertical projection; thus, maximum coverage is 100%. The biological consequences of physical disturbance (rubble turnover, abrasion) are discussed in Chapter 5.

Corals, particularly massive lobate forms, have been found to produce a pattern of growth bands which may be interpreted as seasonal thus being useful in determining the age of individual corals (Knutson et al. 1972). Such banding patterns as seen through

Figure 3. Physical data (water depth and water motion) and coral coverage on a transect originating on the windward reef crest of Johnston Atoll and continuing lagoonward through the rubble zone and into the *Acropora hyacinthus* zone. This transect bisects the study area whose limits are shown by vertical dashed lines. Coral coverage (middle plot) is presented for all species (solid line) and for the vasiform coral, *Acropora hyacinthus* (dotted line). Coral cover is shown as the number of decimeters covered per 5 m^2 expressed as a percentage.

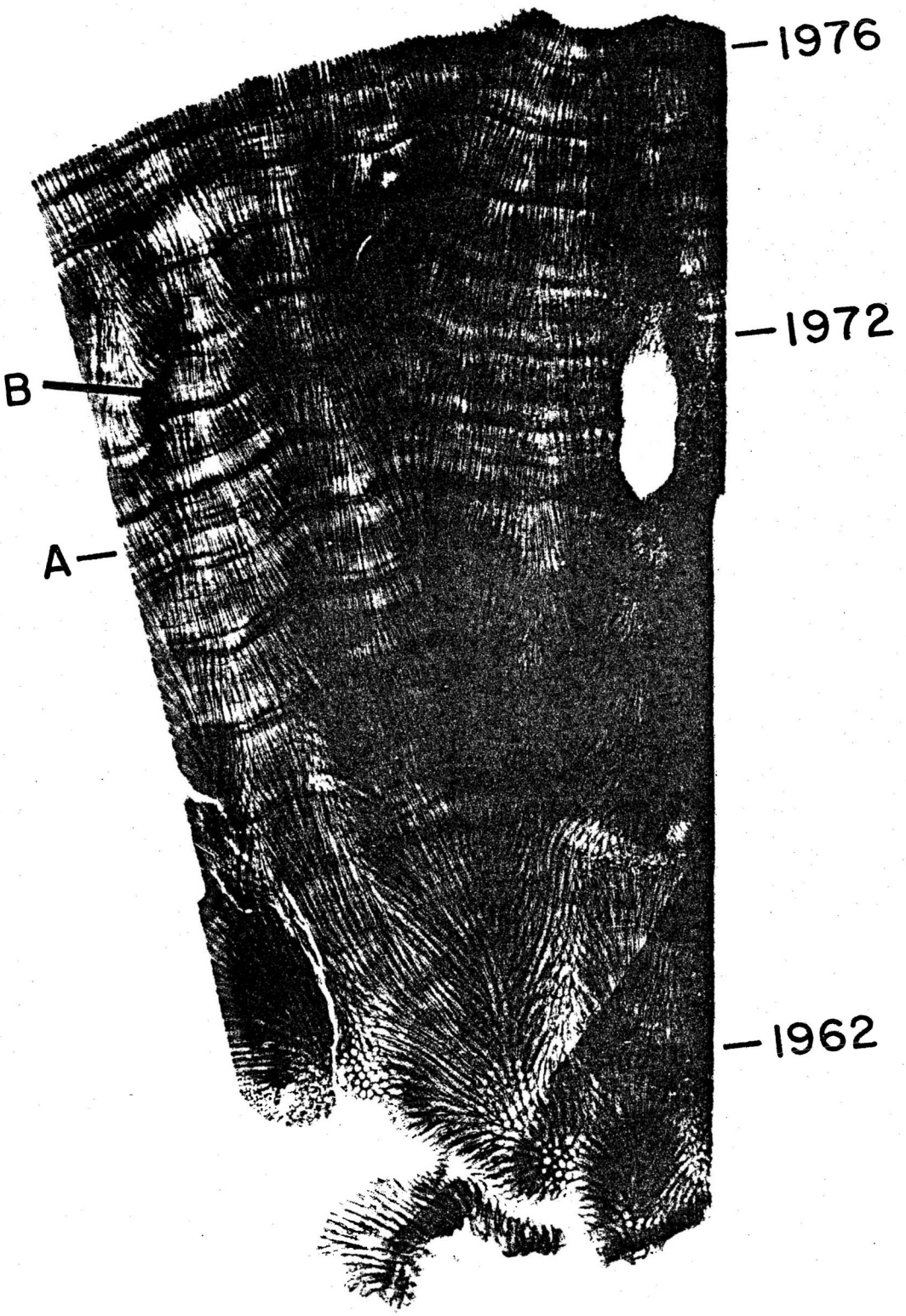

Main Reef Flat
study area
Lagoon
METERS
0
5
Depth
PERCENT COVERAGE
100
20
Coral Coverage
DIFFUSION FACTOR
30
20
10
Water Motion
breakers
strong
surge
moderate current
10
20
30
40
50
60
70
80
90
DISTANCE meters

x-radiographic techniques may represent the organism's physiological response to periodic environmental changes or they may be genetically derived. If patterns of banding are related to the environment, they may provide an insight to the recent physiological history of the individual coral colony and its rate of growth (Buddemeier 1974).

A 28 cm diameter specimen of the coral *Porites lobata* was collected adjacent to the study site at Johnston Atoll on 25 April 1976 for use as a chronometer of recent environmental history in the area. The coral was sectioned and x-radiography performed on two samples using the methods outlined by Knutson et al. (1972).

Plate I presents the x-radiograph positive of one such section. The specimen was estimated to be in its sixteenth year of life at the time of collection. Lunar (monthly) banding is apparent as faint dark lines, "A" in Plate I, as described by Buddemeier and Kinzie (1975). Annual banding is apparent as a thick lighter band (summer, fast growing) followed by a narrow dark layer (winter, slow growing). Two anomalies are present in the coral section in Plate I: one is a hole (a white spot on the positive) caused by a boring organism (*Lithophaga* sp., sipunculan or polychaete) and the second is indicated at "B". The latter irregularity coincides with the only recorded hurricane at Johnston Atoll in which winds attained speeds of 167 km per hour (Amerson and Shelton 1976). The coral may have been temporarily overturned or heavily abraded at that time which resulted in a change in growth. It is unknown how this coral, if overturned, would have been subsequently returned to an upright position. Alternatively, the anomaly may not be real, rather it may simply represent a change in the axis of growth. Buddemeier et al.

Plate I. X-radiograph positive of a section through a 28 cm diameter *Porites lobata* coral collected in April 1976 adjacent to the Johnston Atoll study site in 1.5 m of water. Annual banding (major light-dark series) is evident and lunar bands show up as faint dark lines ("A"). The specimen was in its sixteenth year at the time of collection. A possible explanation for the anomaly at "B" may be the result of the 1972 hurricane. See text for further discussion.


1976
1972
B
A
1962

(1974) were unable to find systematic variations in the dimensions of the low and high density bands in *Porites lobata* that could be related to environmental change. In a recent paper, Isdale (1977) noted that *P. lobata* specimens taken from the same habitat do not show the same growth patterns, thus making inferences on environmental changes as manifested through banding variations of questionable value. In any case, other than the anomaly in the 16 year growth record noted above, there are no irregularities in the Johnston Atoll specimen along the axis studied. This suggests that there has been a certain degree of environmental stability present over the last 16 years for a piece of substratum the size of the coral colony studied here in the windward reef rubble zone.

As previously mentioned, field measurement of actual surface area of the study site was difficult to obtain. Therefore, measurements of the rubble surface exposed to grazing were made using the aluminum foil method (Chapter 3) on rubble removed from a planar area of 0.25 m^2. These measurements resulted in a calculated actual surface of 133 m^2 in the 100 m^2 study area or a surface index of 1.33. Dahl (1973) found surface indices in similar habitats to be between 1 to 1.9. The average piece of rubble at the study site has an exposed surface area of 64 cm^2, and rubble pieces average about 200 per square meter. This greater surface area for grazing coupled with nearby shelter under the vasiform *Acropora hyacinthus* favors a larger herbivore population than would be possible in an area of little relief.

CHAPTER 5

JOHNSTON ATOLL FIELD EXPERIMENTS

Introduction

Quantitative field evidence of the effects of grazers and raspers on coral reef benthic community structure are rare, excepting a few studies where artificial substrata were used (Vine 1974, Birkeland 1977, Day 1977, Brock in press). The use of settlement plates ignores the third dimension, substratum depth, which may alter otherwise acceptable answers to the question "are grazers and raspers important determinants of coral reef community structure?" Since authors cited above showed that grazers and raspers have certain effects on two-dimensional benthic communities, a second question that may be asked is "If benthic surface communities can be altered by rasping fishes, can the underlying cryptobiota be similarly affected?" In this chapter I explore these questions utilizing data collected from the study site located in the windward reef rubble zone at Johnston Atoll.

Materials and Methods

As noted earlier (Chapter 3), field sampling at the Johnston Atoll study site commenced on 27 May 1975 and was repeated on 17 August and 14 October, and on 24 April 1976. Besides gathering visual data (e.g., fish transects and macro-invertebrate censusing), benthic rubble samples were taken from within and adjacent to each

of the three exclusion cages, and from under each of the three roofs. Also, in October 1975 and April 1976 all settlement plates (caged, under roof, and exposed) were removed and replaced with clean plates.

Because sample sorting and organism identification were time consuming, only four control (exposed) and three experimental (caged) natural substratum samples were completely processed. The processed samples came from within and adjacent to the same cage on the four sample dates. No roof samples (shading effect) were processed because visual inspection of a series of roof samples (n = 9) revealed no visible differences from samples exposed to grazing. In the field, parrotfishes were frequently observed feeding on the substratum under the roofs. Only one May 1975 sample representing the commencement of the experiment and thus serving as an initial control was processed. Besides the May 1975 sample, three pairs of subsequently collected samples are reported, each pair consisting of an experimental (caged) sample and a control (exposed to grazing) sample.

Natural rubble samples of similar size were selected for analysis. These substratum samples were all approximately 10 × 10 × 5 cm in size. Upon collection, each rubble sample was placed in a labeled plastic bag and preserved in 10% buffered formalin. In the laboratory each sample was photographed and its surface area determined by use of the aluminum foil method (Chapter 3). Also, volume displacements and wet weights were measured before subjecting samples to acid dissolution of the calcium carbonate matrix to remove the infaunal component of coral rock; organisms were preserved and remained in a readily identifiable state (Brock and Brock 1977). Following

dissolution, plant and animal components were sorted from the organic matrix and identified as far as possible. Subsequently, the animal fraction was oven dried to constant weight for standing crop determinations.

Rough glazed ceramic tiles (∿10 × 10 cm) were used as settlement plates. It was felt that plate immersion in the field for five to six months would be sufficient to see if differences in settlement occurred. Thus settlement plates were collected in October 1975 following a five-month immersion, and in April 1976 after a 6-month immersion period. Each settlement plate was placed in a labeled plastic bag and preserved in 10% buffered formalin.

In the laboratory, settlement plates were first photographed then estimates of algal cover and thickness made using a 15 × 15 cm^2 grid. Algae were distinguished visually only as calcareous-encrusting or as filamentous-mat species. All algal species tended to be very small making identification difficult. The entire upper surface of each settlement plate was scraped with a razor blade into a container where its settled volume was determined. Animals were then separated, identified, and dried for biomass studies. The filamentous algae on the settlement plates tended to trap particles of sand and detritus which was difficult to separate. Following the removal of all animals, the algal-sand fraction was acidified to eliminate calcareous material. The remaining algae were oven dried for an estimate of standing crop.

Every settlement plate and rubble sample was carefully checked for recently settled coral colonies; also the plastic bags containing each sample were rinsed and filtered at the time of processing so as not to lose small epiphytic species that may have fallen off the sample

at the time of collection and preservation. The number of species present in the natural substratum samples have unequal variances thus precluding the use of parametric statistics. Also the number of completed samples are too few to use the appropriate non-parametric paired tests (Siegel 1956) for both the plate and rubble samples.

During each visit to the Johnston Atoll study site all fishes and sea urchins present in a 10 × 10 m area were censused visually using methods outlined in Chapter 3. Fish census data were taken on the experimental reef in Kaneohe Bay for comparative purposes.

Results

The results from the plate study are presented in Appendix Table I and a summary is given in Table 1. Although these data are limited by the small number of completely processed samples, certain trends are obvious. The number of benthic species and individuals are considerably less on plates exposed to grazers (both in the open and under roofs) than for caged plates. Inspection of the exposed plates indicated that epiphytic algae had been grazed heavily. In the field, parrotfishes were seen feeding on these plates and sea urchins probably did also. Both algal and animal biomass was greatest under ungrazed (caged) conditions and least in both exposed treatments as would be expected.

Settlement plates represent a two-dimensional substratum for colonization by benthic species. Coral rubble is rough and porous, thus furnishing a third dimension of habitat space for infaunal species. Appendix Table II presents a taxonomic inventory of organisms found on and in rubble pieces subjected to the two treatments, i.e., grazed

Table 1. Summary from Appendix Table I of observations for the settlement plate experiment conducted at the Johnston Atoll study site. The three treatments in this experiment consisted of plates (10 × 10 cm) exposed to grazing in the open (Exposed), exposed to grazing under a roof of screen (Roofed), and not exposed to grazing (Caged). October plates were immersed for 139 days and April plates for 192 days.

	October 1975			April 1976		
	Exposed	Roofed	Caged	Exposed	Roofed	Caged
Total Number of Plant and Animal Species	6	5	30	7	12	51
Total Number of Invertebrate Individuals	17	3	125	4	40	429
Shannon-Weaver Index (H')	0.75	0	2.35	1.39	1.53	2.59
Total Animal Dry Weight (g)	0.013	0.016	0.041	0.005	0.037	0.518
Total Plant Dry Weight (g)	0.033	0.055	0.281	0.041	0.037	0.654
Calculated Animal Dry Weight (g/m^2)	1.3	1.6	4.1	0.5	3.7	51.8
Calculated Plant Dry Weight (g/m^2)	3.3	5.5	28.1	4.1	3.7	65.4

and not grazed. Table 2, a summary of these data, includes physical and biological characteristics of each of the seven samples processed to date. Among the characteristics is sample porosity defined as the sample volume (by displacement) divided by the wet weight. Also presented is a measure of infaunal habitat complexity which is defined as sample porosity multiplied by its surface area. This measure allows the direct comparison of benthic communities present on and in substratum of differing porosity and surface area. The measure of habitat complexity is discussed in detail below.

The results presented in Appendix Table II and Table 2 are contrary to those found with the settlement plates, i.e., on natural substratum taxonomic richness and numbers of individuals are greater for samples exposed to grazing than for samples protected from grazing. The results for the October 1975 series disagree with the above results; in this case, the protected (caged) sample had a larger number of species and individuals but also had almost twice the porosity (habitat space) as the exposed sample. Taxonomically, polychaetes were the dominant group of organisms present in all of the samples. Their numbers were calculated on a square meter basis for comparative purposes.

Taxonomic richness in terms of the number of phyla present in a sample is plotted against the habitat complexity in Figure 4-A. The total number of individuals present in each natural substratum sample is plotted against the habitat complexity in Figure 4-B. The data points for both caged and exposed samples are closely grouped in this figure suggesting that there are no real differences in the number of individual animals present in a sample of equal habitat complexity,

whether it is caged or exposed to predation. There is, however, a trend for a larger number of animals present in samples with greater habitat complexity than in those with a lower complexity value regardless of exposure. Polychaetes make up over 50% of the number of individuals present in these samples (Table 2). These percentages are highest in the caged samples (caged $\bar{x}$ = 69 ± 4%; exposed $\bar{x}$ = 58 ± 6%). However, plotting the number of polychaete families against habitat complexity (Figure 4-C) for the samples results in no apparent trends at normal field grazing pressures.

Appendix Table III presents data from visual fish transects taken during each visit to Johnston Atoll. Two censuses were conducted at the same time of day in April 1976 to provide information on the variability of the numbers of individuals and species. Fishes were censused under three trophic categories: herbivores, omnivores and carnivores. Table 3 summarizes these data. The variability in the numbers of species and individuals between successive censuses (e.g., 24 and 25 April) is probably due to random encounters with species that have no ties to any particular part of the reef (large predators such as carangids and lutjanids) or to chance encounters with species possessing home ranges and territories that are considerably larger than the 100 m^2 study site.

The census data on sea urchins, a rasping herbivore, in the Johnston Atoll study area is given in Table 4. Five species were encountered over the period of this study. However, only *Tripneustes gratilla* and *Echinothrix diadema* were numerically important. The large fluctuation in the numbers of *T. gratilla* and *E. diadema* cannot be accounted for other than by random movement of sea urchins

Figure 4. The relationships between habitat complexity (sample area x porosity) and the numbers of phyla (A), of organisms (B), and of polychaete families (C) from seven natural substratum samples that were either exposed to (open circles) or protected from (black squares) grazing and rasping organisms.

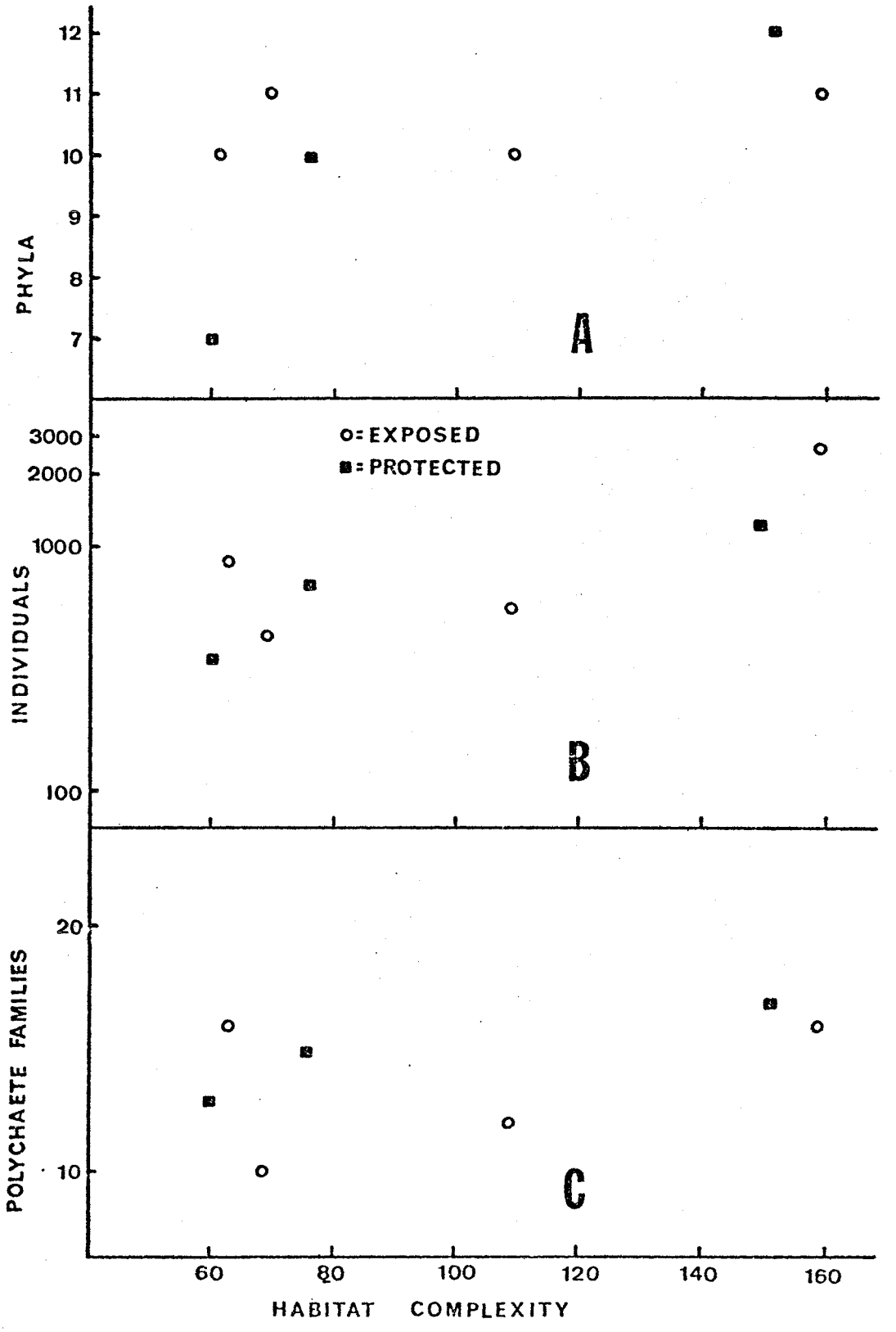

PHYLA
12
11
10
9
8
7
A
INDIVIDUALS
3000
2000
1000
100
o = EXPOSED
■ = PROTECTED
B
POLYCHAETE FAMILIES
20
10
C
60
80
100
120
140
160
HABITAT COMPLEXITY

Table 2. Physical and biological attributes of 4 grazed (exposed) and 3 ungrazed (caged) substratum samples from Johnston Atoll. Sample porosity is the sample volume divided by the sample wet weight. The habitat complexity is porosity multiplied by sample surface area. Sample wet weight and volume displacement values include the substratum and all associated organisms. Data are summarized from Appendix Table II.

	COLLECTION DATE						
	May 1975	August 1975		October 1975		April 1976	
TREATMENT	Exposed	Caged	Exposed	Caged	Exposed	Caged	Exposed
Factor:							
Sample Size (surface area cm^2)	107	114	136	136	156	146	299
Sample Wet Weight (g)	250	341	438	382	503	775	714
Sample Volume Displacement (ml)	160	180	200	425	350	400	375
Sample Porosity	0.64	0.53	0.46	1.11	0.70	0.52	0.53
Habitat Complexity	69	60	63	151	109	76	159
No. of Countable Animals	444	355	873	1318	570	703	2709
No. of Phyla	11	7	10	12	10	10	11
No. of Individual Polychaete	244	236	561	886	293	523	1657
Estimated No. of Polychaetes/m^2	22800	20700	41250	65150	18780	35820	55410
By No. % Polychaetes	55	66	64	67	51	74	61
Calculated Animal Dry Wt. (g/m^2)	3.7	14.9	8.1	5.2	9.6	19.2	3.2

Table 3. Summary from Appendix Table III of the visual fish censuses conducted in the 100 m^2 study site at Johnston Atoll. These data are presented by trophic group (herbivore, omnivore and carnivore) as well as by total numbers of species and individuals encountered. Summary information is given on parrotfish (Scaridae) abundance and the Shannon-Weaver index of diversity (H') has been calculated for each census period.

	Sampling Date				
	May 1975	August 1975	October 1975	24 April 1976	25 April 1976
No. of Individuals	175	381	265	584	539
No. of Species	28	35	35	42	37
Shannon-Weaver (H')	2.69	2.75	2.81	2.42	1.87
No. Parrotfish Individuals	38	101	53	323	346
Percent Parrotfish	22	27	20	55	64
Herbivores					
No. of Individuals	123	289	184	511	492
No. of Species	10	13	13	13	15
Carnivores and Omnivores					
No. of Individuals	52	92	81	73	47
No. of Species	18	22	22	29	22

Table 4. Abundance of five species of sea urchins in the 100 m^2 study site at Johnston Atoll. The 24 and 25 April censuses were conducted 23 hours apart.

Species	Sampling Date				
	27 May 1975	17 August 1975	14 October 1975	24 April 1976	25 April 1976
Tripneustes gratilla	83	5	8	141	135
Echinothrix calamaris	1	9	18	4	4
E. diadema	49	81	100	101	106
Heterocentrotus mammallatus	1	1	0	0	0
Echinometra mathaei	0	0	0	1	1
Total	134	99	126	247	246

throughout the habitat or by periodic spawning aggregations. A small amount of movement is suggested in the April censuses taken 24 hours apart. The maximum density of adult *T. gratilla* and *E. diadema* from 3 to 6 urchins/m^2 (personal observations). Generally such densities are seasonal and occur when gonads of the sea urchins are well developed or recently spent, suggesting that the aggregations may be related to spawning. The gonads of sea urchins at Johnston Atoll were not examined, thus the reasons for large fluctuations in standing crops there are unknown.

Discussion

The settlement plates used in the above experiment are a two-dimensional system in which predation in the form of grazing may retard the development of the benthic community. Removal of this predation by caging results in a more diverse benthic community development. Paine (1966), Dayton (1971), Menge and Sutherland (1976), and Connell (1978) have noted that some disturbance (predation) can lead to the development of a more diverse benthic community than otherwise found. Moderate disturbance may result in patchiness or habitat heterogeneity; extreme disturbance or none may lead to a uniform habitat with concurrent lower species diversity (Paine 1966).

The low-diversity benthic community that developed under normal grazing pressures in the field is a consequence of the two-dimensional nature of the plates. Coral rubble (natural substratum) samples from the study site harbored a more diverse epifaunal and infaunal community under similar field grazing pressure than was observed in the absence of grazing and rasping. Natural substratum samples provide a third dimension through surface texture and porosity, which may serve as refuges or simply add more space.

An important resource to any such benthic community is space. Space may be measured both by surface area determinations as well as by porosity (internal space) of the substratum. Surface area is important not only to species whose life cycles are confined to surfaces but also to the infaunal component of the benthic community in that these species must at some stage of their life cycle pass over and through the water-substratum interface. The establishment and

maintenance of an infaunal community may be influenced by the porosity of the substratum (internal surface area). The porosity is a function of the previous history of the substratum (e.g., hardness of the parent coral material, whether it is reconsolidated material, what previous borer species have reworked it, etc.). These two aspects of the space resource (porosity and surface area) may be multiplied to give an index of habitat complexity for benthic species.

Parrotfishes and sea urchins are primarily responsible for the removal of benthic species at Johnston Atoll. This information is based on visual censuses, extensive field collecting, observation, and gut content analyses. Many other herbivorous fishes were observed feeding within the study site, but they are specific in their food requirements and generally do not affect the benthic animal communities while feeding (see Hiatt and Strasburg 1960, Jones 1968*a*, Hobson 1974, Ogden and Lobel 1978 for reviews). I recognized six species of parrotfishes and five sea urchin species in the Johnston Atoll study area. Visual censuses showed that parrotfishes were numerically important, averaging 1.7 individuals/m^2 (range 0.3 to 3.5/m^2). The wet weight of parrotfishes averaged about 36 g/m^2 (range 8-60 g/m^2). In the study area sea urchins have the same mean density (1.7 urchins/m^2) and ranged from 1 to 2.5 individuals/-m^2. On the experimental patch reef in Kaneohe Bay (Chapter 8) parrotfishes occurred in a density of 1.1 fish or 10.8 g/m^2 and no sea urchins were present. This reef received the perturbation of sewage and stream runoff which was reflected in a lower diversity of organisms relative to the Johnston study site. It is shown experimentally in Chapter 7 that parrotfishes at field densities in Kaneohe

Bay may be important in determining the structure of the benthic community.

A second factor (other than predation) affecting benthic communities is physical disturbance of the substratum. With extreme water motion, rubble is moved about; this physical turnover results in the decimation of the sessile epilithic component. Disturbance whether manifested by predation (Paine 1966, Dayton 1971, Virnstein 1977) or by rock turnover (Osman 1977, 1978) can increase local species diversity if it is intermediate in intensity (Menge and Sutherland 1976, Connell 1978). The effect of rock turnover at the Johnston Atoll study site has not been addressed in the present study, but it does occur as evidenced in October 1975 when one of the exclusion cages was found partially buried under about 15 cm of rubble. For the purposes of this study, it is assumed that rubble within the exclusion cages is exposed to the same frequency of turnover as that outside of the cages.

A relatively high frequency of substratum turnover and abrasion may be responsible for the low coral coverage seen in the windward reef rubble zone at Johnston Atoll. Young corals (to 1 cm) often were encountered on the rubble, but substratum instability probably inhibits their survival. Such a habitat favors species that are capable of rapid colonization and possess short lifecycle characteristics (see Sutherland and Karlson 1977). Many of the microalgae probably are well suited to this type of environment. The greater numbers of herbivorous fishes and sea urchins encountered in the rubble zone than elsewhere at Johnston Atoll are probably related to the continuous band of open space with nearby shelter and microalgal

resources. These attributes, in turn, result from physical disturbance (see previous chapter).

Data presented above suggest that the effect of rasping parrotfishes and sea urchins in normal field densities may appreciably alter the benthic community structure in two-dimensional systems. Addition of the third dimension appears to reverse this effect. It is postulated that the benthic community present on and in coral rubble in the Johnston Atoll study site has evolved maximum organism diversity under this herbivore and turnover impact. Furthermore, the presence of a third dimension gives the epifaunal (and infaunal?) components the opportunity to survive by providing refuges.

CHAPTER 6

FOOD RESOURCE PARTITIONING BY PARROTFISHES

Introduction

Parrotfishes have received much attention in the literature on tropical reefs because of their purported role in feeding on corals (Randall 1974). There is, however, little quantitative data on food preferences for members of the family Scaridae. This is due in part to the difficulty of identifying and quantifying ingested food material because it is pulverized by the pharyngeal mill, a structure characteristic of the parrotfish family Scaridae. Parrotfishes typically have a rasping beak (Plate II) which is used in scraping hard substrata for food materials (Plate III). Once ingested, all food passes into the pharyngeal mill consisting of opposing teeth set in the pharyngeal bones. These teeth compress, pulverize and triturate all materials. Posterior to the pharyngeal mill is the esophagus, separated from the intestinal tract (duodenum, ileum and rectum) by a pyloric valve (Gohar and Latif 1959).

Some quantitative information exists on what parrotfishes consume; the most pertinent summaries are found in Al-Hussaini (1947, 3 Red Sea species), Hiatt and Strasburg (1960, 9 Marshallese species), Randall (1967, 10 Caribbean species) and in Hobson (1974) who examined 3 species of Hawaiian parrotfishes. None of these studies have addressed the question of the possible impact that parrotfishes may have on structuring benthic communities through their feeding

nor have they found food resource partitioning among the Scaridae. In this chapter data from gut content analyses on parrotfishes will be used to attempt to answer the following questions:

1. Does food resource partitioning occur among the common Hawaiian parrotfishes?
2. Do parrotfish ingest benthic invertebrates while feeding on benthic algal resources?
3. Do these fishes utilize potential food resources that occur within coralline substrata? These resources include the boring algae "*Ostreobium*" (Odum and Odum 1955) and the cryptofauna which collectively are termed the cryptobiota.

Materials and Methods

Parrotfishes were collected by spear and poison (rotenone) for gut content analysis at Johnston Atoll in the windward reef rubble zone during each visit. Scarids also were taken in Kaneohe Bay on patch reefs by use of a fence net and by spear. Upon collection all fishes were tagged, injected with and preserved in 10% neutralized formalin. In one case, the specimens were frozen.

Laboratory procedures began with the determination of standard length, wet weight, sex, and gonad maturation of each specimen. The intestinal tracts were removed and the esophagus was separated from the gut. The contents of each section were emptied into graduated cylinders with buffered formalin and allowed to settle for several days to obtain an initial volume of material. Settled material was then acidified with nitric acid (to no greater than 4% by volume) to remove all calcium carbonate. The residue was filtered on a

stainless steel geological screen (63 μ porosity), rinsed gently to remove the acid, and then centrifuged for 15 to 30 seconds (7100 RPM maximum) to obtain an estimate of the initial volume of calcium carbonate present.

Digestion (breakdown) of materials appears to proceed rapidly along the entire length of the gut (Gohar and Latif 1959); therefore, in the microscopic examination of gut contents for organisms consumed, only acidified materials taken from the esophagus anterior of the pyloric valve were used. For the quantification of these materials a sample was pipetted and placed in a 50 × 20 mm counting cell under a stereo-microscope (at 250X magnification). The marks on a linear ocular micrometer were used as a set of points with which the point intersect method of sampling was used (method similar to Jones 1968*b*). The material in the counting cell was stirred and items were enumerated until 100 points had been sampled per fish. These data yielded the percentage of items found in food categories: "algae," "animal" or "unknown." Because gut materials had been so finely ground, more detailed categorization usually was impossible. Following the point counts, each slide was thoroughly scanned and notes taken on identifiable pieces of food items. All material was retained for future reference.

Non-acidified materials from the esophageal region of several parrotfishes (*Scarus perspicillatus* and *S. sordidus*) were compared to gut contents that had been treated with acid to remove the calcium carbonate fraction. Food items (bits of algae or animals) were more readily seen and identified in the acidified material than in the samples with the calcium carbonate slurry. An attempt was made to

find a method of staining the acidified gut residue differentially to distinguish plant from animal material. However, no satisfactory technique was found.

Besides using the above point-intersect method for determining food consumed, many field observations of parrotfish feeding behavior were made. Additionally, grazing rates were obtained by following individual scarids in situ, during different times of the day and for a measured period of time (5 to 10 minutes), noting the time spent in feeding. Also five plastic panels (PVC, 18 × 18 cm) were placed horizontally at five locations on two patch reefs in Kaneohe Bay at depths less than 2.5 m. Initially clean panels were left for a 14-day period, then collected and examined for characteristic scrape marks left by feeding parrotfishes (see also Plate III). Feeding marks on ten 1 cm^2 areas were counted on the upper surfaces to estimate the number of bites made per unit of time in field situations.

To study the possible use of the "*Ostreobium* layer" (boring algae, Odum and Odum 1955) and the surface microflora by *Scarus*, parrotfishes of different sizes were held in clean aquaria. Selected pieces of coralline rock substratum initially were sampled with a cork borer (for the *Ostreobium* layer to 1 cm in depth) or by scraping a known area of surface with a scalpel blade to obtain samples for chlorophyll-*a* analysis. These pieces of substratum were placed in aquaria with parrotfishes and were later removed and resampled for chlorophyll-*a*. Chlorophyll-*a* was extracted from the *Ostreobium* layer following the technique outlined by Odum and Odum (1955), and analyzed by method of Strickland and Parsons (1968).

Results

Field evidence suggested that *Scarus sordidus* is the most abundant of the small parrotfish species (maximum S.L. about 270 mm) and *Scarus perspicillatus* is one of the most common large parrotfishes (to about 450 mm S.L.) at both Johnston Atoll (Chapter 5) and in Kaneohe Bay (Chapter 8). Therefore, emphasis was placed on these species in the analysis of gut contents. Other species examined included *Scarus dubius* (3 specimens), *S. taeniurus* (1 specimen) and *Calotomus sandvicensis* (2 specimens). These latter species were rarer and not easily collected. Table 5 presents the gut content data in summary form. After having passed through the pharyngeal mill, food materials are well triturated making identifications extremely difficult. The last column in Table 5 (% unknown) is a catchall primarily for the following materials, e.g., mucus (probably generated by the intestinal mucosa of the parrotfishes), small fragments of boring sponges (*Cliona* spp.) and algae (*Ostreobium* spp.) all of which are difficult to identify. Animal remains noted in Table 5 include pieces of harpacticoid copepods, mysids, amphipods, shrimps, sponges (*Cliona* spp.), bryozoans, tunicates, micromollusks, foraminiferans, and most commonly, polychaetes.

Food materials listed in Table 5 suggest a division amongst these five parrotfish species. *Scarus perspicillatus, S. sordidus* and *S. taeniurus* have more calcium carbonate present and less algal material than *Scarus dubius* and *Calotomus sandvicensis*. These differences may be related to variations in dentition in these species which is discussed later.

Table 5. Synopsis of gut content analyses performed on five species of scarids collected from the rubble zone at Johnston Atoll and in Kaneohe Bay over a three year period. Species below were collected in both localities except for the single *S. taeniurus* taken in Kaneohe Bay. The column headed by "% Unknown" refers primarily to boring algae, sponge and mucus found in the intestinal tract of these parrotfishes. Where applicable, standard deviations are included.

Species	Number Examined	Standard Length Range (mm)	Average % $CaCO_3$ by Volume	Point Intersect Gut Analysis (Average of Percent Occurrence)		
				% Algae	% Animal	% Unknown
Scarus sordidus	15	115-253	70±11	15±6	4±2	79±9
Scarus perspicillatus	11	119-355	62±22	15±7	7±4	78±9
Scarus dubius	3	156-208	58±13	26±6	6±2	69±7
Scarus taeniurus	1	140	63	13	10	77
Calotomus sandvicensis	2	205-355	46±4	38±3	14±8	49±11
All Species	32		64±16	18±8	6±4	76±11

Of the total organic material ingested (all parrotfishes combined), the identifiable animal component made up about 6% by occurrence and algae only about 18%. Calcium carbonate, on the other hand, averaged over 60% of the volume of materials consumed. Calcium carbonate was not measured by the point intersect method for it had been dissolved prior to this analysis. I have observed feeding parrotfish in the Hawaiian Islands, Johnston Atoll, Marshall Islands (Kwajalein, Utirik, Rongelap and Enewetak Atolls), Caroline Islands (Truk), Great Barrier Reef (at Lizard Island) and the Straits of Malacca (Port Dickson, Malaysia). At all of these localities, parrotfishes of all sizes actively appear to select coralline substrata whose surface is characteristically covered with a fine algal mat comprised of microphytic algae (e.g., *Jania, Pocokiella, Liagora, Microdictyon, Neomeris, Laurencia, Herposiphonia, Polysiphonia, Chondria*).

Panels placed in the field for information on the feeding rates of parrotfishes yielded a mean value of 13 ± 8 tooth marks (bites)/cm^2 (n = 50) over a 14-day period. Assuming that parrotfishes began feeding immediately on these surfaces and fed continuously from morning (0600 hours) until twilight ($\sim$1900 hours) everyday, we may calculate the feeding rate to be 714 bites/m^2 per hour or 0.9 bites/cm^2 per day. In reality the panels are probably not acceptable as a feeding surface until an algal film has appeared (3 to 4 days). If we assume that it takes 3 days to develop the algal film then the feeding rate is 909 bites/m^2 per hour or 1.2 bites/cm^2 per day.

My underwater observations in Kaneohe Bay and at Johnston Atoll suggest that parrotfish spend 60% of their active day or 8 hours feeding at these localities. A visual census of the parrotfishes

residing on one of the reefs where panels were placed (see Chapter 8) at the time of this experiment resulted in a density of scarids of 0.8 parrotfishes/m^2 of planar reef surface. Thus 0.8 parrotfishes made 11,800 bites/m^2 in 88 hours of actual feeding or 168 bites per fish per square meter per feeding hour. These calculations all assume that scarids do not feed preferentially on the plastic panels over natural substrata.

Besides gut content analyses and field observations, algal resource use by parrotfishes may be measured by the reduction of chlorophyll-*a* over time in experimental situations. Surface chlorophyll-*a* (from the microflora) was measured from coralline rocks taken in the field. Rubble removed from adjacent to the study site at Johnston Atoll resulted in a mean chlorophyll-*a* value of 0.63 ± 0.36 $\mu g/cm^2$ (n = 15). Ten samples taken from an area relatively free of grazing fishes and sea urchins in Kaneohe Bay had an average chlorophyll-*a* value of 7.44 ± 3.63 $\mu g/cm^2$. The magnitude difference between these average values may be attributed to differences in the microfloral species composition, to differential grazing pressure, to eutrophication or to a combination of these factors.

Two aquarium experiments were conducted using rubble to observe the effect of parrotfish feeding on surface algae and the *Ostreobium* layer. The subsurface *Ostreobium* layer is very patchy in its distribution resulting in "noisy" (large variance) data for the small number of samples taken. There are no evident patterns or trends in these data. Parrotfishes at high experimental densities can appreciably reduce the surface algae present in coralline substrata (Chapter 7). Two trials using Kaneohe Bay rubble yielded a

consumption rate of chlorophyll-*a* by parrotfishes of 4.9 to 9 µg chlorophyll-*a* per gram (wet weight) of parrotfish per day.

Discussion

The results of the gut content analyses indicate that the five species of scarids studied here are utilizing very nearly the same food resources thus making it difficult to separate the species by trophic differences. This suggests that (a) differential utilization of food materials by these parrotfish species is very subtle, or (b) that the food resources are sufficiently great that there is no competitive interaction and hence no ecological separation by way of food. The parrotfish specimens used in these analyses have come from two very different habitats in the Hawaiian faunal region (the Johnston windward reef rubble zone and Kaneohe Bay, Oahu) and were collected at different times throughout the year thus tending to reduce any bias due to seasonal variation in food habits.

A source of error in quantitative estimates of the gut contents of many fish species with a varied diet is due to a longer retention of hard than of soft parts of prey. This leads to a bias favoring those hard parts in quantitative studies (Randall 1967). This source of error is important in certain groups, e.g., carnivores (Brock 1972), but is probably of little consequence in the parrotfishes which thoroughly grind all food materials with their pharyngeal mills.

The fused teeth that form a beak (Plate II) and the presence of a pharyngeal mill allow parrotfishes to bite off chunks of coral rock and grind them into fine sediment. In doing so, all surface algae become well triturated and infaunal or cryptobiotic components are

likewise exposed. The cryptobiotic resource is comprised of boring algae (*Ostreobium* spp.), boring sponges (*Cliona* spp.), nematodes, polychaetes, mollusks, bryozoans and crustaceans (see Chapter 5). Ongoing research by the author on coral reef cryptobiotic communities indicates that the biomass of these organisms may range from 10 to 1,400 g (dry weight)/m^2 of bottom with a mean value of about 50 g/m^2 in most Hawaiian and Johnston reef areas. Generally, polychaetes comprise a substantial proportion of the total biomass. The cryptobiotic resource is probably not directly tapped by many fish species besides the parrotfishes; few other fishes have the dentition and morphological adaptations necessary to get into the coralline substratum. Parrotfishes do rasp into the coralline substratum while feeding as evidenced in photographs of tooth scars on the substratum (Plate III, Cloud 1959, plate 130; Bakus 1967, p. 140 and Hobson 1974, p. 996) and by the presence of abundant calcium carbonate in the digestive tract. Emery (1956) examined two specimens of *Scarus perspicillatus* from Johnston Atoll and obtained 25% coral, 65% coralline algae and 10% fine debris by volume; thus the contents were composed of about 90% calcium carbonate (no methodology given). Cloud (1959) did not describe methods used but stated that these grazing fishes contribute between 4.25 to 6.18 metric tons of calcium carbonate sediment per hectare of reef area per year. Similarly Bardach (1961) found that the total non-nutritive component of grazing and rasping fish gut contents to be 2 to 4% of their body weight in the Caribbean. He estimated that these reef raspers produce 2300 kg of calcium carbonate sediment per hectare per year. Randall (1967) found that five Caribbean species of *Scarus* had an average of 69% coralline

Plate II. Side views of (A) *Scarus perspicillatus* (male, 370 mm S.L.) and (B) *Calotomus sandvicensis* (male, 296 mm S.L.) showing the divergence of beak structures. The teeth in *S. perspicillatus* are totally fused forming heavy dentition while the teeth of *C. sandvicensis* are not.

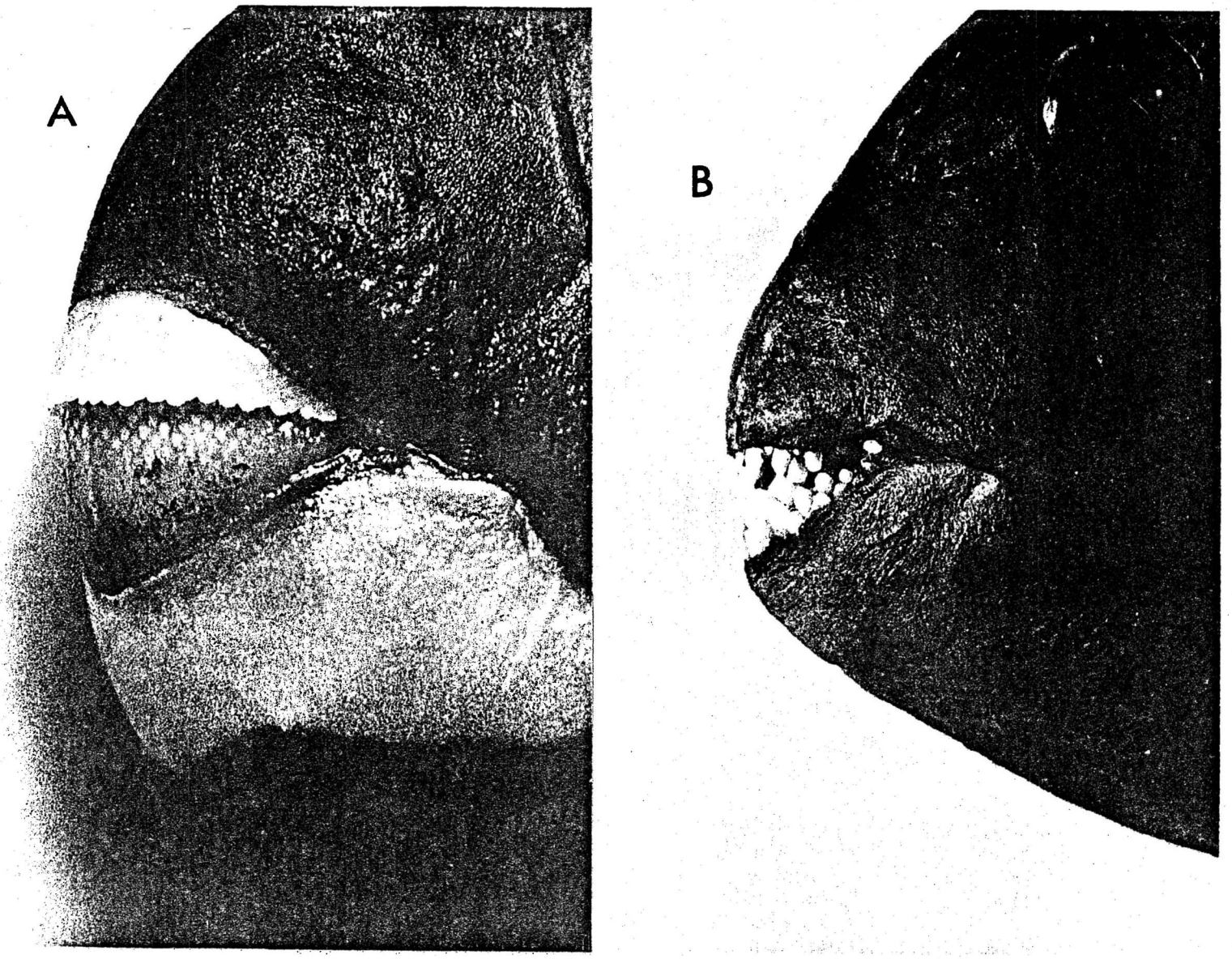

A
B

Plate III. Parrotfish tooth scars caused by feeding on coralline substratum from an intertidal location on the windward reef flat at Enewetak Atoll, Marshall Islands in the upper photograph (courtesy of P.L. Jokiel) and on basalt substratum from a 10 m depth offshore of Kaneohe Bay, Oahu in the lower photograph. Algae present on both samples includes a number of microphytic species as well as *Schizothrix* sp. on the Enewetak sample and encrusting coralline forms on the Kaneohe Bay sample. The upper photograph is about one third natural size; in the lower photograph the field of view is magnified about 3 times.

material by volume in their intestinal tracts. Data from the present study suggests that the diet of parrotfishes in Kaneohe Bay and at Johnston Atoll contains about 65% calcium carbonate (Table 5).

Exposed macro-invertebrates other than corals and echinoids are few on coral reefs (Bakus 1964, 1966, 1967). The animal remains encountered in the gut contents of scarids (Table 5) are probably species associated with the algal mat or species with cryptofaunal habits. These organisms probably are ingested incidentally but serve as a protein source. At all of the above locations overturning the substratum by hand attracts numerous fishes including scarids all of which feed on the exposed invertebrates. Under these circumstances particularly in undisturbed habitats (Johnston, Enewetak and Rongelap Atolls) parrotfishes have been observed feeding on exposed serpulid polychaetes, ascidians, tunicates, bryozoans and sponges, essentially clearing the overturned rock of all sessile invertebrates within minutes. Bakus (1964, 1967) has observed the same phenomenon at Fanning Island and at Enewetak Atoll.

Nothing was found to suggest differential selection of food items related to the size of the parrotfish in the range of individuals examined in this study. Rather, once the appropriate substratum is located (preferably solid limestone with a veneer of fine algae) parrotfish appear to be non-selective in their feeding, consuming whatever is available. Such non-selective consumption would probably be limited by jaw size and structure; thus, small parrotfish would not be able to consume some organisms that large individuals might take.

There has been a long-standing controversy over whether scarids feed on live corals or just rasp algae and cryptofauna from

the hard substratum. This controversy began with Darwin's (1845, 1890) observations at Coco-Keeling Islands that these fishes feed on live corals. Forbes (1885) made the same observation at the Coco-Keeling Islands. Finckh (1904) at Funafuti in the Ellice Islands determined that parrotfishes feed on algae only. Verwey (1931) noted that three scarid species at Batavia were algal feeders but Al-Hussaini (1947) listed four species of *Pseudoscarus* in the Red Sea as coral feeders. Suyehiro (1942) recorded one Japanese species as feeding only on algae. Newell et al. (1951) in the Bahamas and Newell (1956) found that Tuamotuan scarids fed on algae and took a layer of limestone in doing so; in the Gilbert Islands Cloud (1952) noted the same thing. Emery (1956) at Johnston Atoll found that coral made up 25% of the stomach contents of *Scarus perspicillatus* and Hiatt and Strasburg (1960) in the Marshall Islands recorded 9 parrotfish species (including *Scarus sordidus*) feeding principally on corals. Gohar and Latif (1959) ascertained that coral was a major constituent of the food of three parrotfish species in the Red Sea. Stephenson and Searles (1960) on the Great Barrier Reef found no coral in the stomachs of three scarids and Choat (1966) never saw parrotfishes at Heron Island feeding on live corals. In the West Indies Randall (1967) determined that of 10 species of parrotfishes examined only two species had a very small amount of live coral present in their stomachs. Glynn (1973) has seen one scarid species feeding on corals off the Pacific coast of Panama and Glynn et al. (1972) list three species from the same locality as coral feeders. Hobson (1974) found no evidence of coral feeding amongst scarids examined off the Kona, Hawaii coast; however, Randall (1974) notes that *Scarus perspicillatus* does

occasionally feed on live coral in the Hawaiian Islands. *Scarus perspicillatus* has been seen by this author feeding on the coral *Porites lobata* seaward of Kaneohe Bay in 10 m of water on one occasion and twice along the Kona, Hawaii coast. Parrotfishes have not been observed feeding on live corals at Johnston Atoll in the present study. In conclusion, coral feeding by parrotfishes in the Hawaiian Islands or at Johnston Atoll appears to be a rare occurrence.

A large amount of flocculent mucus was present in the intestinal tracts of all parrotfishes examined in this study. This mucus was not apparent until the gut contents were acidified, otherwise this material was not readily discernible in the calcium carbonate slurry. Hobson (1974) stated that fish species which feed on live corals characteristically have abundant mucus present in the gut contents presumably derived from the coral; he presents no supportive evidence. Reese (1977) presents excellent visual documentation of coral feeding in two *Chaetodon* species (photographs of nematocysts and zooxanthellae from stomach contents). Since the present study of gut contents found nothing to indicate feeding on live coral by parrotfishes (no zooxanthellae, nematocysts or other cnidarian characters), it is suggested that the mucus found in the gut contents is generated by the fish and used as an aid to digestion and passage of the calcium carbonate slurry. Hiatt and Strasburg (1960) reported "coral polyps" in the gut contents of 83% of the *Scarus sordidus* examined by them in the Marshall Islands. Considering the effectiveness of the pharyngeal mill of scarids in grinding all materials to a fine slurry (Cloud 1959, Bardach 1961, Randall 1967, 1974), the finding of recognizable coral polyps in the gut contents seems questionable.

Generic separation of *Calotomus* from *Scarus* is based partially on differences in the dentition (Schultz 1958, Gosline and Brock 1960); *Calotomus* has free, imbricate, incisor-like teeth whereas in *Scarus* the teeth are fully coalesced into a parrot-like beak (Plate II). The dentition and jaw structure of *Calotomus sandvicensis* is not as heavy as that of *Scarus perspicillatus, S. sordidus* or *S. taeniurus*. Differences in dentition suggest differences in food and feeding strategy. Indeed *Calotomus sandvicensis* in the present study has the most divergent of diets (the least calcium carbonate by volume and the greatest percentage of identifiable algae and animal material). *Scarus dubius* has the typical fused beak of *Scarus*, however the teeth and jaw structure are less massive relative to *S. perspicillatus, S. taeniurus*, and *S. sordidus*. These differences were also reflected in the diet; *Scarus dubius* took in more identifiable plant material and less calcium carbonate than the other *Scarus* species studied. These data suggest that *Scarus dubius* and *Calotomus sandvicensis* feed on similar materials which are probably more restricted to the surface of coralline rock (more plant material and less calcium carbonate) than the food materials consumed by *Scarus perspicillatus, S. sordidus* and *S. taeniurus*. The greater proportion of calcium carbonate slurry present in the gut contents of the latter species suggests that they utilize the cruptofaunal-*Ostreobium* layer to a greater extent than do other fishes.

Bardach (1961) found that scarids spend two-thirds to four-fifths of the day feeding which is about 8.5 to 10.4 hours per day assuming a 13-hour day. He determined also that juvenile scarids passed food materials in one to two hours following ingestion, middle

sized individuals (250 to 500 g wet weight) retained food materials for three to five hours and that large individuals (greater than 1000 g wet weight) turned over their intestinal contents but once a day. The considerable time spent feeding (about 60% of the daylight hours) along with relatively short retention time suggests that not much energy is derived on a per unit time basis by scarids feeding on a coralline substratum. There are, however, relatively few other fishes that use the coralline substratum and cryptobiota directly as a food resource.

CHAPTER 7

LABORATORY STUDIES ON THE EFFECTS OF GRAZING BY PARROTFISHES AND ROLE OF REFUGES IN BENTHIC COMMUNITY STRUCTURE

Introduction

Two laboratory experiments were undertaken because of the lack of definitive results from the field data on the effects of grazing (Chapter 5). The first experiment (microcosm experiment number 1) endeavored to answer the question "is benthic organism diversity and biomass affected by the feeding activities of *Scarus*"? The second experiment attempted to elucidate the effects of refuges and parrotfish density on benthic species richness and biomass, as well as determine if parrotfish could be serving as keystone species in the structuring of benthic communities.

Materials and Methods

The first experiment was conducted from 22 September through 22 December 1976 in a fiberglass aquarium located outdoors and exposed to ambient sunlight conditions. The tank was 90 × 90 cm in surface area and 40 cm deep. A plastic screen (mesh size 1 × 1 cm) was used to bisect the tank diagonally. Unfiltered seawater taken from the adjacent reef flat at the Hawaii Institute of Marine Biology was allowed to flow through the tank (at ∿10ℓ/minute) for a week before the introduction of herbivorous fishes. Three healthy heads

of the coral *Pocillopora damicornis* all approximately 10 cm in diameter, were placed in each half of the aquarium. These coral heads served as a source of larvae for coral recruitment in areas both exposed to and protected from grazers. Each head was free of most dead basal material. This coral was introduced on the day following the initial filling of the tanks. *Pocillopora damicornis* is able to reproduce in a normal lunar cycle over an annual period under laboratory conditions (Edmondson 1946, Harrigan 1972).

After one week of seeding the tank with meroplankton coming in via the seawater system, three *Scarus sordidus*, all roughly 10 g in weight, were placed into one side of the tank. At the conclusion of the experiment 91 days later, each side of the tank was sampled for benthic organism diversity and biomass. Sampling consisted of taking five 100 cm^2 scrapes with a scalpel blade from the walls on both the grazed and ungrazed surfaces. Of the five samples collected in each treatment, two were taken at 10 cm and three at 20 cm below the surface (see Appendix Tables IV and V). All samples were labeled and preserved in 10% formalin. Samples were sorted under a dissecting microscope, organisms identified and dried at 100°C until constant weight was attained (2 to 5 days).

The second experiment, to test the effect of refuges and grazing pressure (*Scarus* density) on benthic community structure, commenced on 19 July 1977 and ran for 43 days at the Hawaii Institute of Marine Biology. The experiment was carried out in nine 550 ℓ microcosm tanks (117 × 117 × 40 cm) each exposed to full natural light and receiving unfiltered seawater from the adjacent reef flat at approximately 10 ℓ/minute. The physical, chemical and biological

characteristics of the microcosm system were described by Henderson et al. (1976) and Evans (1977).

Two terracotta tiles (31 × 23 cm) were placed in each tank; pieces of plastic screen of three mesh sizes and thickness, e.g., fine mesh (4 × 4 mm) 1 mm thick, medium mesh (5 × 5 mm) 1.5 mm thick and coarse mesh (6 × 7 mm) 2 mm thick were used as refuges for benthic organisms. The screen was cut to 10 × 20 cm pieces which were laid flat and tied to the terracotta tiles. The treatments on the tiles included a non-screened exposed portion or control. These settlement plates were placed against the tank walls such that all refuges and controls were accessible to feeding scarids. The tiles along with 15 *Pocillopora damicornis* colonies (average weight per tank = 4133 g) were placed in each microcosm tank a week before the fish were introduced. This seven day period served as a time for the settlement of benthic organisms, recruited from the meroplankton in the incoming water. The coral heads were weighted in a tared vessel of seawater using the technique outlined by Bak (1973) and Jokiel et al. (1978), at the beginning of the experiment. Juvenile *Scarus* (probably *Scarus taeniurus*) were individually weighted in tared vessels of seawater and placed in the microcosms after the seven day seeding period (average weight ∿10 g). Density treatments of *Scarus* assigned to tanks ranged from 1 to 8 fish and a control (0 fish).

At the termination of the experiment the fish were again weighed to obtain an assessment of growth. Also chlorophyll-*a* samples were collected, estimates on algal coverage of wall surfaces were made, and the refuges were sampled. Chlorophyll-*a* was sampled

by carefully scraping with a scalpel blade all the material from a 100 cm^2 area on the wall of each tank, placing it in 90% acetone and freezing until analysis was made following the method of Strickland and Parsons (1968). Counts of all *Pocillopora damicornis* settlements were taken on the walls of the microcosm tanks and estimates of the percentage cover of filamentous and calcareous algae were made. The two terracotta plates in each tank were sampled as follows: each plate was carefully lifted out of its tank and a 10 × 10 cm portion of the screen serving as a refuge was cut away. Organisms remaining on the tile under the screen were scraped from the 10 × 10 cm area and preserved in 5% neutralized formalin along with the 10 × 10 cm piece of screen. A 100 cm^2 sample was scraped from the exposed portions of the tile. Organisms were removed from the screen under a dissecting microscope and where possible all individuals sorted to species and counted. For dry weight determinations, organisms were grouped into higher taxa (Family, Class, or Phylum) and dried at 100°C until constant weight was attained.

These data were analyzed for relationships among the variables using multiple regression techniques.

Results

A summary of the findings for the first experiment are presented in Table 6. The species list, number of individuals encountered, and their dry weights are given in Appendix Tables IV and V. The variances of the number of species between the two treatments (exposed and protected) were checked with an F test and found to be equal ($F = 6.91$, n.s.). A t-test of the mean number of species under

Table 6. Comparison of benthic communities occurring on surfaces exposed to and protected from grazing parrotfishes over a 91 day period. The number of benthic species, and individuals and their dry weight are presented for five samples collected under each treatment at the termination of the experiment. Each sample (scrape) was 100 cm^2 in area. Complete data are presented in Appendix Tables IV and V.

Condition	No. Species	No. Individuals	Calculated Dry Weight (g/m^2)
NOT GRAZED			
Scrape 1	22	269	522
Scrape 2	33	1,327	1,246
Scrape 3	28	464	1,069
Scrape 4	36	3,558	1,066
Scrape 5	27	216	436
GRAZED			
Scrape 1	1	1	2.7
Scrape 2	2	2	1.4
Scrape 3	6	32	10.4
Scrape 4	5	10	0.7
Scrape 5	3	3	3.4

the two treatments (protected and exposed) yielded significant differences ($P < 0.001$, 2-tailed test); therefore, the feeding activities of three parrotfish had a significant influence on the number of species found in the benthic community. The most important taxa present in both exposed and protected benthic communities were polychaetes, bivalve mollusks, and small arthropods.

The second experiment explored the effects of grazing on the composition and biomass of benthic communities under different densities of fish and refuge conditions. Data from this second experiment are summarized in Table 7 and the results of the refuge

Table 7. Summary of microcosm grazing experiment number 2. Effects of variable *Scarus* stocking densities on fish growth and development of benthic food resources (community development) after 36 days (cf. Figures 5, 6, and 7). See text and Appendix Tables VI through XIV for details of methodology and results.

Number of Fish per Tank	Total Fish Biomass at Start (g)	Net Weight Gain per Fish		Number of Coral Recruits	Macroalgae, Percent Coverage		Benthic Biomass ($g/100\ cm^2$) Dry Weight	Chlorophyll-*a* ($\mu g/100\ cm^2$)
		g per Fish	% Gain		Calcareous	Non-Calcareous Filamentous		
0	0	0	0	719	0	10.0	1.02	93.1
1	34.3	0.8	2	1044	0	5.3	0.09	108.0
2	36.5	2.0	11	160	0	7.5	0.08	80.5
3	39.7	3.2	24	302	0	16.3	0.06	155.4
4	75.6	3.0	16	193	0	22.5	0.07	227.6
5	80.2	3.9	24	101	1.0	5.0	0.10	121.9
6	58.2	0.1	1	98	3.5	0	0.08	65.8
7	80.0	-0.6	-5	7	2.3	0	0.03	90.7
8	83.2	-0.2	-2	20	1.8	0	0.04	78.7

experiment carried out on terracotta tiles are listed in Appendix Tables VI through XIV. Species diversities given in these appendices are based on the Shannon-Weaver index of diversity,

$$H' = -\sum_{i=1}^{k} Pi \log Pi$$

where Pi is that proportion of species i present in a sample and k is the number of species.

Figures 5, 6 and 7 graphically present some of the data given in Table 7. Chlorophyll-*a* values peaked under a grazing pressure of four *Scarus* (Figure 5) as did the percentage of filamentous algal coverage (Figure 6-C). The *Scarus* collectively gained weight over their 36 days of residence in the microcosm tanks up to a density of five fish (Figure 7-B); densities greater than five fish or 1 g wet weight per 600 cm^2 of feeding area were detrimental to growth. At these higher densities coralline algae (Figure 6-B) supplanted filamentous algae (Figure 6-C). The biomass of benthic organisms exposed on the walls of the microcosm tanks decreased from the zero fish treatment to the one grazing fish treatment; at all higher grazing densities the biomass of exposed benthic animals remained low (Figure 7-C). An early colonizer and only major herbivore recruited from the influent seawater was the sea slug *Stylocheilus longicauda* which decreased in numbers and weight at *Scarus* densities greater than three fish (Figure 7-A). These sea slugs were constantly recruited to the system. Settlement of colonies of coral on the exposed walls decreased at higher fish densities (Figure 6-A).

Figure 5. Amount of chlorophyll-*a* ($\mu g/100\ cm^2$) present on microcosm walls after 36 days of exposure to grazing by different numbers of juvenile parrotfish.

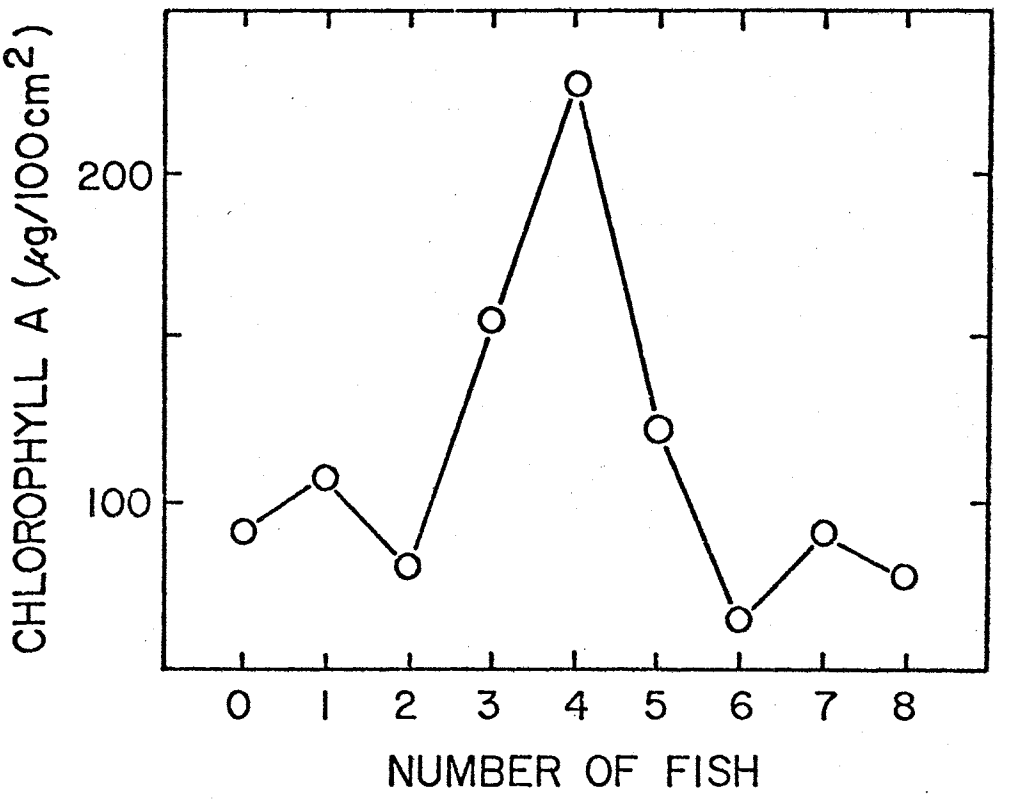

CHLOROPHYLL A (μg/100cm²)
200
100
0
1
2
3
4
5
6
7
8
NUMBER OF FISH

Figure 6. Number of coral settlements (A), the percentage of encrusting coralline algal coverage (B), and the percentage of filamentous algal coverage (C) on 1.76 m^2 of settlement space under nine densities of *Scarus* grazing for 36 days in the microcosm experiment.

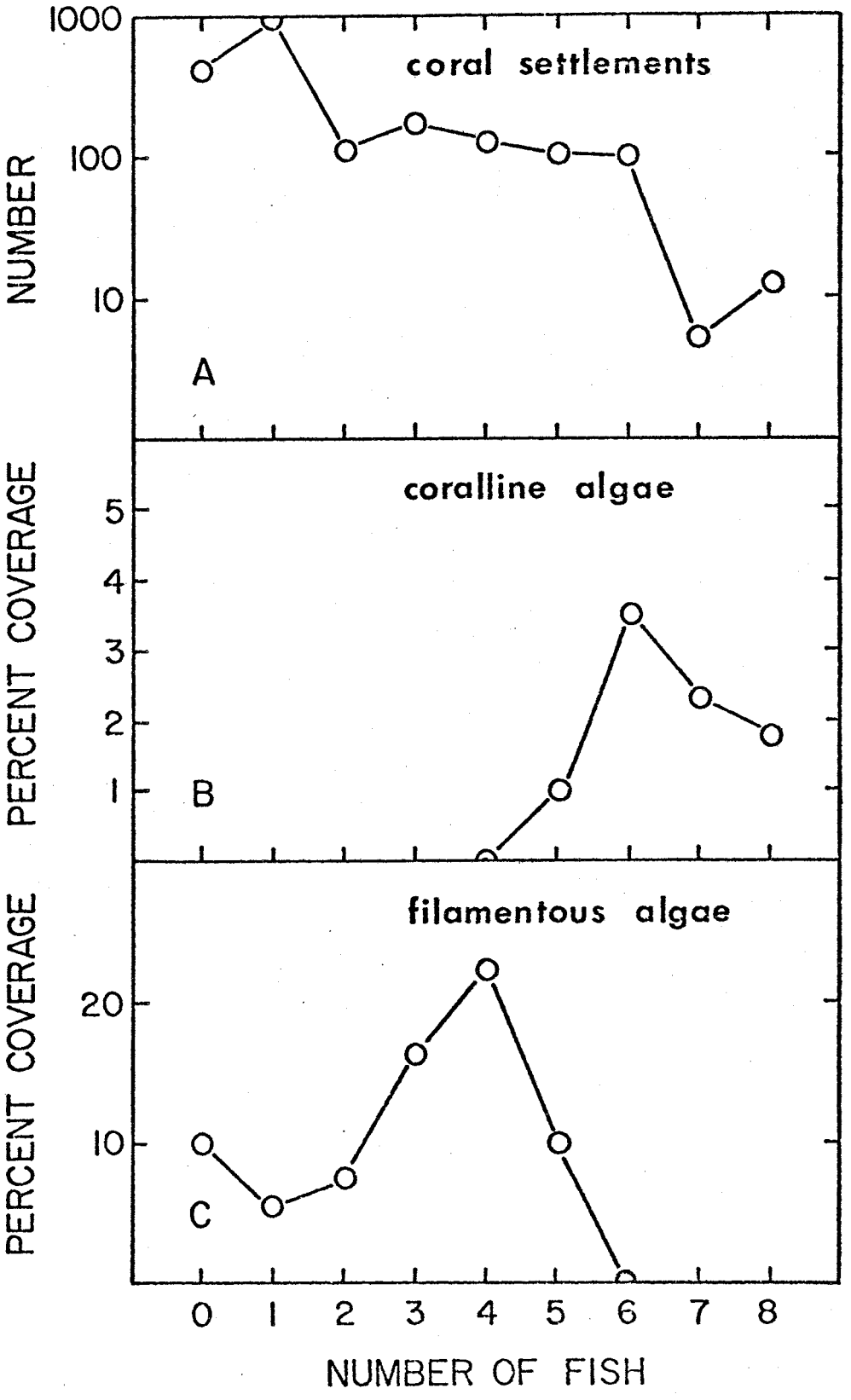
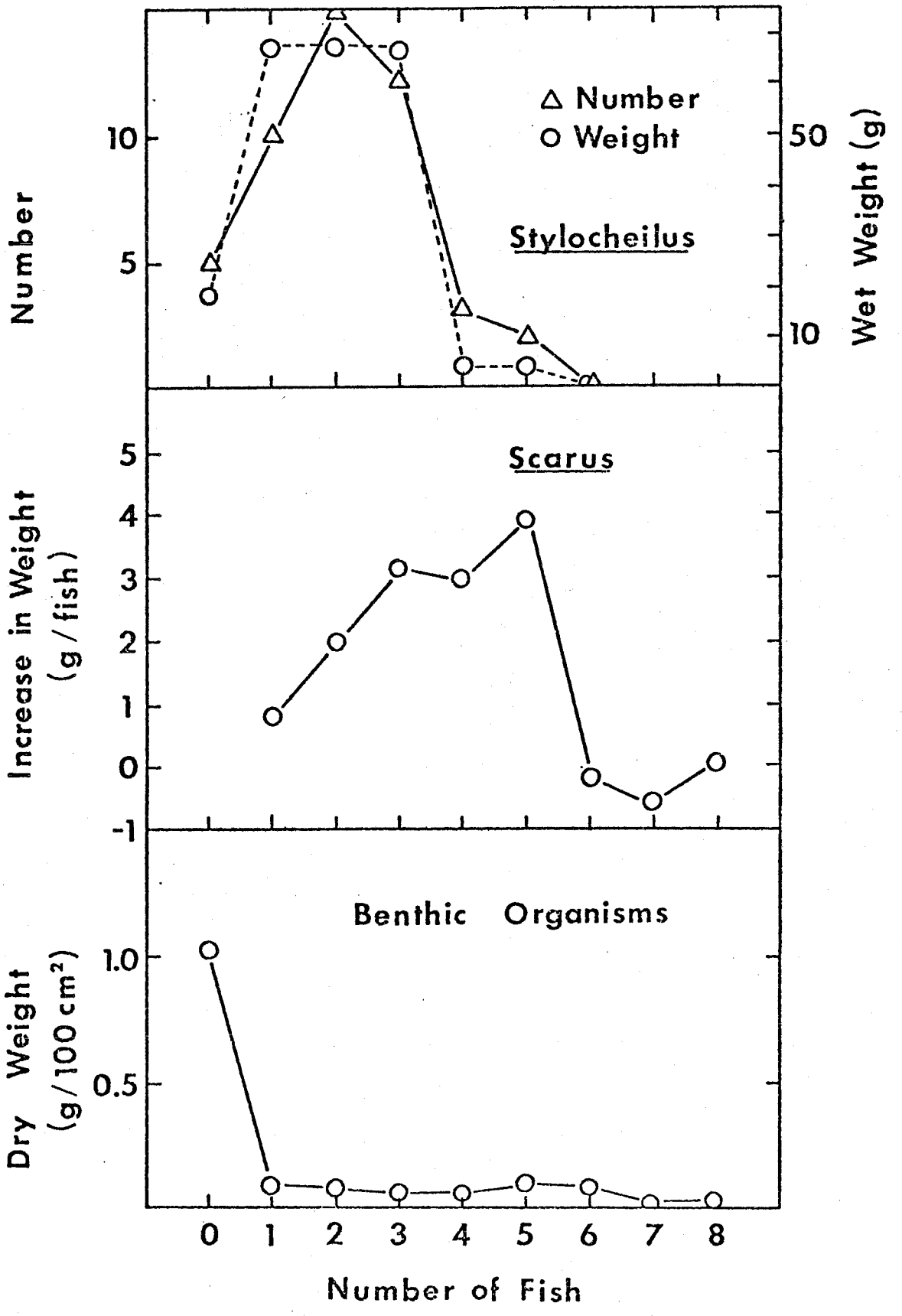

1000
100
10
NUMBER
coral settlements
A
5
4
3
2
1
PERCENT COVERAGE
coralline algae
B
20
10
PERCENT COVERAGE
filamentous algae
C
0 1 2 3 4 5 6 7 8
NUMBER OF FISH

Figure 7. Effects of different degrees of *Scarus* grazing (number of fish) after 36 days in tanks on: A, the number and weight of sea slugs (*Stylocheilus longicauda*) present; B, gain in fish weight; and C, biomass of benthic organisms developing on tank walls.


Number
Wet Weight (g)
△ Number
○ Weight
Stylocheilus
Scarus
Increase in Weight (g / fish)
Benthic Organisms
Dry Weight (g/100 cm²)
Number of Fish

In the second experiment, refuges were quantified by the mesh size and the thickness of the screen material. In general, the larger screen dimensions (mesh sizes) provided better refuges for benthic species. Exposed terracotta plates received a zero refuge rating, fine mesh with 16 mm^2 holes was given a value of 16, medium mesh a value of 25 (25 mm^2 mesh openings) and coarse mesh, a value of 42. This numerical rating of refuge space enabled the use of stepwise multiple regression to verify relationships amongst the variables of refuges and the density of grazing fishes against the variables of the number, biomass and diversity of benthic species as well as the number of coral recruits. The results of this analysis are given in Table 8. These analyses indicate that the number of benthic species depends significantly on the amount of protection (the refuge effect) and the number of grazing fish. The biomass of benthic species, the species diversity (H') and the number of successful coral settlements are also significantly dependent on the refuges and the number of grazing fishes (Figures 8, 9, 10). Increased grazing pressure has a negative effect on the number of species, biomass, and diversity of benthic invertebrates but positively affects the number of coral recruits. As might be expected, all of the dependent variables are enhanced by increasing the refuges.

Discussion

Under exposed conditions filamentous algae decreases at higher fish densities and calcareous algae becomes a more important component of the substratum. Filamentous algae are more dominant at a density of four fish which probably explains the peak chlorophyll-*a*

Table 8. Results of multiple stepwise regression analysis of 4 dependent variables versus the independent variables of refuges and number of grazing *Scarus*. Only the independent variables which yielded regressions significantly different from zero at the 1% level (based on the F value shown) and only those which accounted for 5% of the total variation in the data are given. Double asterisks indicate a highly significant F value ($P < 0.01$).

Dependent Variable Y	Variable Entered X	Multiple Correlation Coefficient	% of Variance Explained by X	F Value To Enter	Computed Equation
CASE 1 Number of Benthic Species	Amount of Exposure or Refuges (X_1)	0.83	69%	76.5**	$\hat{Y} = 14.37 + 0.56X_1 - 0.80X_2$
	Number of Fish (X_2)	0.86	5%	45.5**	
CASE 2 Biomass of Benthic Species	Amount of Exposure or Refuges (X_1)	0.58	33%	16.8**	$\hat{Y} = 1.59 + 0.05X_1 - 0.06X_2$
	Number of Fish (X_2)	0.62	5%	10.2**	
CASE 3 Species Diversity (H')	Amount of Exposure or Refuges (X_1)	0.76	58%	46.9**	$\hat{Y} = 1.85 + 0.02X_1 - 0.04X_2$
	Number of Fish (X_2)	0.79	5%	27.8**	
CASE 4 Number of Coral Recruits	Amount of Exposure or Refuges (X_1)	0.48	23%	10.1**	$\hat{Y} = 1.05X_1 + 0.21X_2 - 2.10$
	Number of Fish (X_2)	0.63	17%	11.0**	

at this density (see Figures 5, 6-B and 6-C). It is interesting that *Scarus* growth is also enhanced at these intermediate fish densities (Figure 7-B). The experimental evidence suggests that the growth of both the parrotfish and filamentous algae are positively correlated and there may have been an evolution in both groups to coexist at these levels of grazing. Data collected on the Kaneohe Bay experimental reef in 1977 (Chapter 8) indicate that there was 1.1 *Scarus* (10.8 g wet weight) per square meter. These densities are similar to those found in the optimal situation in the microcosm tanks (0.6 to 1.5 *Scarus*/m^2 or 9 to 17 g of *Scarus*/m^2 of substratum). The density figures taken from the microcosm data do not include the effects that competing herbivores and predators might have on *Scarus* in the natural situation. Other than *Stylocheilus longicauda*, a herbivore, which is normally rare in the field, competitors and predators were absent in the microcosms. Also, the surface areas given for the field data are planar determinations, no consideration is given here to actual surface area due to reef surface irregularities. Little information on the density of *Scarus* on reefs is available in the literature. Bakus (1967) found one scarid per 123 m^2 of reef at Enewetak Atoll and Randall (1963) in the Caribbean found that scarids greater than 250 mm S.L. occurred in densities of one fish per 27 to 46 m^2.

The increase in calcareous algae at higher fish densities in the experimental situation may in the field have important consequences to the stability and structure of reefs. Vine (1974) noted that in feeding, grazing fishes were able to keep the filamentous algal growth down making the coralline algae competitively superior. This same author recognized the importance of the cementing action of these

algae in maintaining the structural integrity of the reef. Not only are calcareous algae important to the physical structure of a reef but they provide suitable substrata for colonization by hermatypic corals (Harrigan 1972, Birkeland 1977), which are a principal geological component of coral reefs. Thus, by their grazing activities, *Scarus* are probably very important to the maintenance and character of their reef ecosystem.

Algae were almost non-existent in the refuges of the microcosm experiments. The apparent lack of algae is probably due to (a) the success of many benthic species in the refuges that do not allow algal holdfasts on their surfaces (sponges, tunicates) and/or (b) that other unseen benthic herbivores were present in the system. The refuges added a third dimension to an otherwise planar settlement plate; the effect is one of enhancing species richness and biomass (see Figures 8 and 9). Also evident from the refuge experiment is that *Scarus* do remove benthic invertebrates in their feeding (Figure 7-C, 8, and 9). The increased habitat heterogeneity due to refuges results in less effective predation on the benthic community by *Scarus* than is seen on exposed surfaces (Figures 8 and 9). Additionally, this predation in both the exposed and refuge habitats results in an increase in benthic species and biomass up to moderate levels of predation, e.g., 2 to 5 fish per tank or 1 g of predator (wet weight) per 0.66 to 0.11 m^2 of feeding surface. These data support the contention that predation in structurally simple environments first increases and then decreases diversity as it increases in intensity (Paine 1966, 1971, 1974, Paine and Vadas 1969, Harper 1969, Emlen 1973, Menge and Sutherland 1976, Day 1977, Lubchenco 1978, Brock, in press). The

Figure 8. The number of benthic species per 100 cm^2 encountered under different refuges (exposed-open circles, fine mesh-black squares, medium mesh-black circles and coarse mesh-open triangles) and grazing pressure (0 to 8 *Scarus*) for 36 days in the second microcosm experiment.

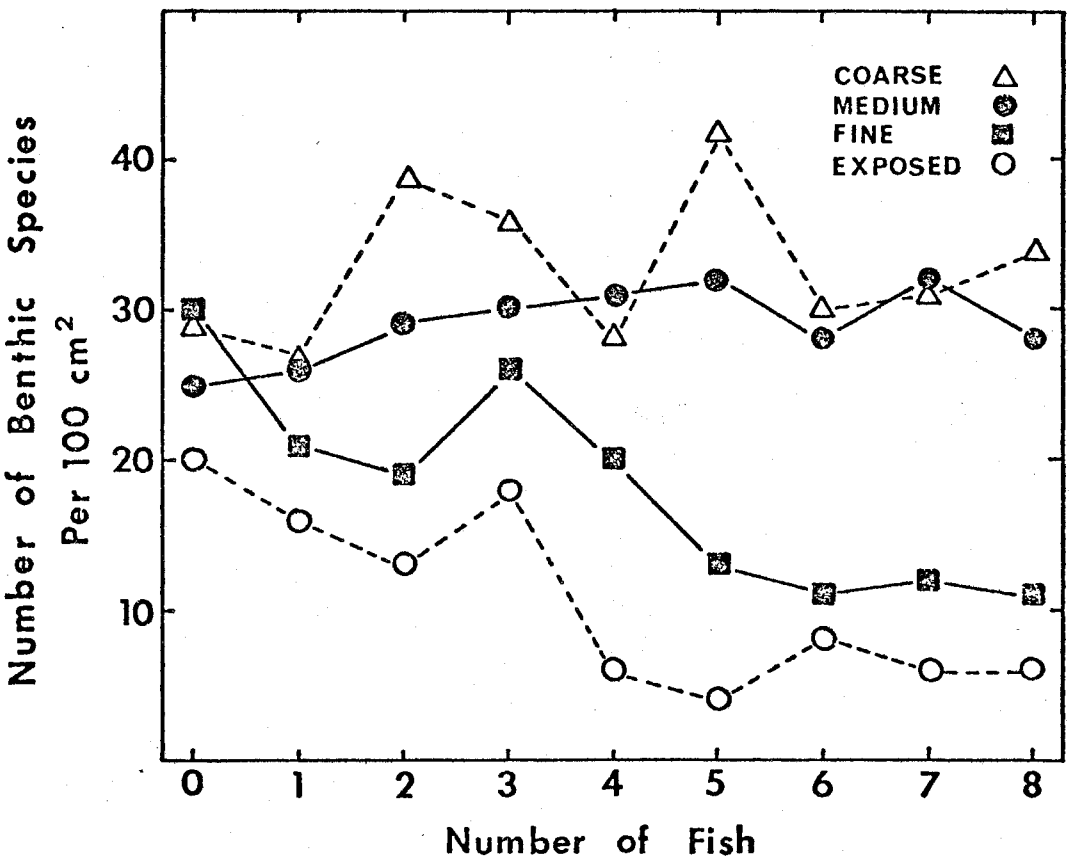
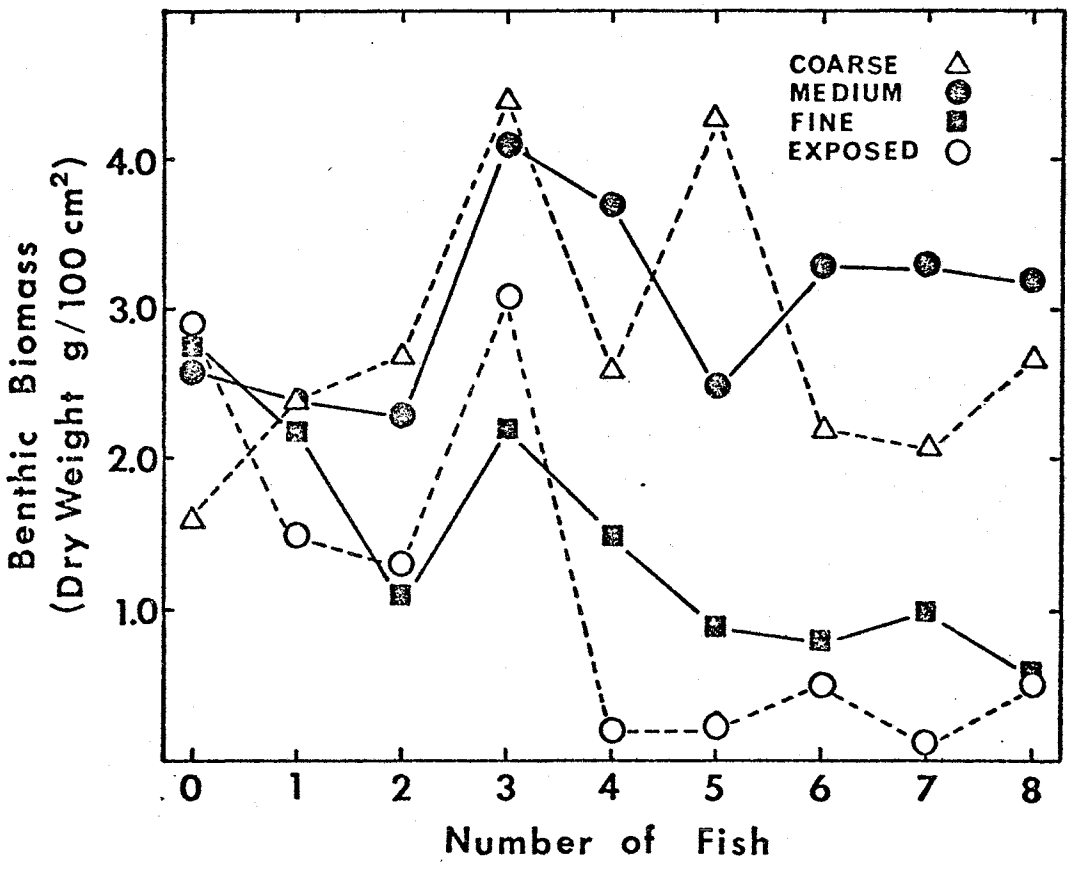

COARSE
MEDIUM
FINE
EXPOSED
Number of Benthic Species
Per 100 cm²
40
30
20
10
0
1
2
3
4
5
6
7
8
Number of Fish

Figure 9. Plot of the biomass of benthic organisms (dry weight g/100 cm^2) under different refuges (exposed-open circles, fine mesh-black squares, medium mesh-black circles, and coarse mesh-open triangles) and grazing pressure (0 to 8 *Scarus*) for 36 days in the second microcosm experiment.

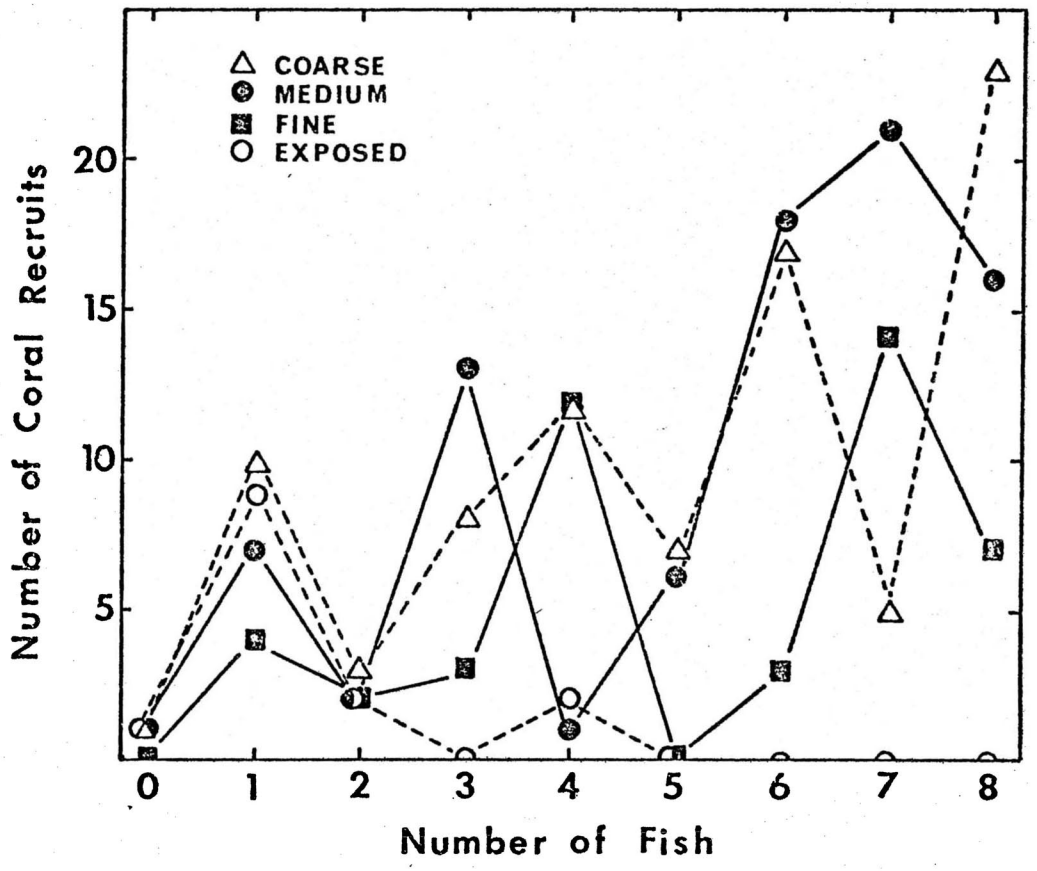

COARSE
MEDIUM
FINE
EXPOSED
Benthic Biomass
(Dry Weight g/100 cm²)
4.0
3.0
2.0
1.0
0
1
2
3
4
5
6
7
8
Number of Fish

increase in substratum complexity (from exposed plates to the coarse mesh refuges) could allow greater species packing by better habitat segregation (niche compression hypothesis, MacArthur and Wilson 1967, T. Schoener 1974*a*, 1974*b*) or the refuges may simply provide an escape from predation for the benthic species (Woodin 1978). These experimental results lend support to the field observation that exposed benthic species other than corals are rare on tropical reefs (Bakus 1966) and that grazing parrotfish may be partially responsible (Bakus 1964).

Coral recruitment is enhanced by refuges (Figure 10) as well as by increased grazing pressure (Table 8). The refuges act to lower predation and provide more space for settlement. Increasing the grazing pressure probably increases the space available for settlement of benthic species. Many authors have implicated the grazing and rasping activities of fish and echinoderms in clearing space for coral settlement (Bakus 1966, 1969; Dart 1972, Porter 1974, Randall 1974, Birkeland 1977, Potts 1977). There is a point beyond which grazing and rasping becomes detrimental to corals. This point is related to the density of fish and the intensity of feeding which may be linked to the available food supply. Also, the size of the predator may cause a shift in the size of prey consumed. Large *Scarus* will consume sessile prey that small parrotfish will avoid. In the microcosm experiments small fish ($\sim$10 g) were used which avoided coral colonies greater than 6 to 8 polyps in size.

Small *Scarus* were used in these experiments because in the field (both Kaneohe Bay and at Johnston Atoll) the small individuals are most numerous. For example, in a sample (N = 495) of all sizes

Figure 10. The number of coral recruits present in each of four refuges (exposed-open circles, fine mesh-black squares, medium mesh-black circles and coarse mesh-open triangles) after 36 days of grazing by *Scarus* at different densities (0 to 8 fish).


COARSE
MEDIUM
FINE
EXPOSED
Number of Coral Recruits
20
15
10
5
0
1
2
3
4
5
6
7
8
Number of Fish

comprised of 3 species from a number of localities in Kaneohe Bay, the mean wet weight was 22 g. Thus, corals or any benthic invertebrate species that initially grow quickly may be able to escape predation by virtue of their size (Paine 1976) in such a system. Many species of corals have been shown to have high initial growth rates that level off with time (Vaughan 1916, Mayor 1918, Edmondson 1929, Stephenson and Stephenson 1933, Boschma 1936, Matoda 1940). However, Connell (1972) has shown that some species grow at a constant rate.

In summary, the microcosm experiments suggest that low densities of parrotfishes cause benthic community structure to proceed to macroalgal dominance; at intermediate levels of grazing intensity (0.6 to 1.5 fish/m^2 or 9 to 17 g wet weight/m^2) a diverse community develops which may be enhanced by the presence of refuges. At *Scarus* densities greater than 1.9 fish or 20 g wet weight/m^2 and in the absence of refuges, the benthic community develops low diversity and biomass. These optimum densities relate well to field estimates made on the experimental reef in Kaneohe Bay (Chapter 8) where *Scarus* occur at 1.1 fish/m^2 or 10.8 g wet weight/m^2. Parrotfishes are the major rasper found on this reef; no sea urchins have been encountered there. The data are not so clear for the Johnston Atoll study site. There, six *Scarus* species average 1.7 fish or 36 g wet weight/m^2. However, sea urchins were abundant in the study area, occurring at an average density of 1.7 urchins/m^2 with an estimated wet weight of 438 g/m^2. The evidence suggests that parrotfishes are important in the structuring and maintenance of reef communities that are dominated by corals and calcareous algae. *Scarus* serves as the

keystone species sensu Paine (1969) in Kaneohe Bay and probably shares this role with sea urchins at the Johnston Atoll study site.

Newell (1971) stated the lithothamnion-scleractinian reefs underwent a major development and radiation during the Eocene about 50 million years ago leading to reef communities as we know them today. During this same period, acanthopterygian fishes radiated into the fishes that inhabit modern reefs (Patterson 1964, Hobson 1974). Among these evolving fishes were the Scaridae. If parrotfishes are indeed as important in structuring coral reef communities as the experimental evidence above suggests, then perhaps their activities are partially responsible for the physical and biological structure of modern shallow water coral reefs.

CHAPTER 8

STABILITY AND STRUCTURE OF A CORAL PATCH REEF FISH COMMUNITY

Introduction

Previous chapters indicate the importance of rasping and grazing fishes to the maintenance of benthic community structure on coral reefs. There are, however, many unanswered questions concerning the community composition and stability of these herbivores. Some of these questions are:

1. What happens to a coral reef in the absence of all rasping and grazing fishes?
2. If these fishes are all removed from an isolated patch reef, how does recolonization proceed?
3. What are the number and biomass relationships of these herbivores to other trophic levels on a given reef?
4. How effective is the visual transect method in assessing diurnally active coral reef fishes?

In this study an attempt was made to answer these questions by removing and ascertaining the community structure of the fishes inhabiting an isolated patch reef in Kaneohe Bay and following subsequent recolonization.

Materials and Methods

The patch reef selected for this experiment is located in the

central sector of Kaneohe Bay (Figure 2). It is shaped like an inverted cone, the flattened subcircular top having an area of about 490 m^2. The reef is isolated from the nearest neighboring reef, 130 m to the leeward, by relatively deep water (12 m) overlying a fine mud bottom. The lower sides and the middle of the top of the reef are covered with rubble; live coral is restricted to the upper sides and rim of the reef. The rubble slope is steep and unstable, presenting a poor substratum for corals, and lacks shelter for larger fishes. Most of the reef crest area is dominated by the bubble alga, *Dictyosphaeria cavernosa*. The top of the reef has a diameter of roughly 25 m and at low tide is about 30 cm below the surface. A slightly larger reef with similar structure and located 400 m to the northeast was chosen as a control.

In August 1966 the experimental reef was depopulated of its fishes as part of a study by Wass (1967). To eliminate the escape and loss of fishes, a fine-mesh (2 cm stretched) net, 150 m long and 11 m deep was quickly set around the reef base at the 9 m contour. The net enclosed a planar area of about 1500 m^2. Once the net was in place, 55 kg of 5% rotenone powder was mixed to a paste and spread throughout the entire enclosed area. Fishes killed by the rotenone were picked up and transported to the laboratory where they were wet weighed and preserved. Wass (1967) followed the recolonization on the experimental reef for 241 days and used the same control reef as in the present study.

In October 1977 the same procedure was used to remove all fishes on the same experimental reef. A day of calm weather was chosen so that wind induced currents and waves would not disperse

the poison. The entire process (net setting, rotenone spreading, fish retrieval and net removal) took about six hours. About 40 people participated in the project. Fish were weighed wet, measured (standard length), tagged and preserved in 10% formalin. Species diversity indices were calculated for collections using the Shannon-Weaver index of diversity (H').

Fish census by visual transect was conducted two weeks before the depopulation experiment and continued at periodic intervals. The day following rotenone application, a fish census and a careful examination for dead fishes was made on the experimental reef. The reef slope and mud lagoon floor below the depth where the net was set down was searched for fishes. The only relief present in this area was a few large pieces of dead coral. A census was made of the few fishes residing in this area. Just prior to depopulation, substratum samples were taken for epi- and infaunal analyses. Also, a series of 1 m^2 permanent quadrats were set up on the top and sides of the reef to monitor algal changes in the absence of fishes.

Fishes removed from the experimental reef were classified into six feeding categories: herbivore, planktivore (feeding on zooplankton), omnivore, carnivore (feeding on animals other than zooplankton and coral), detritivore, and coral feeder (feeding on coral polyps and/or coral mucus). The fishes in the latter two categories were minor in numbers and biomass (Appendix Table XV) and were excluded from further analysis. The food habits of most species were obtained from the literature; where these habits were unknown, specimens were examined. In cases where no food remains were found, fishes were not classified by food habits.

Results

The number and wet weight of each fish species collected both in the present study and by Wass (1967) are presented in Appendix Table XV. There were 76 species taken in 1966 and 81 species recovered in 1977 from the experimental reef; of the 112 species collected in the two studies, only 45 (40%) were common to both. A total of 33 families of fishes were collected with 22 (67%) common to both studies. The fishes in Appendix Table XV are classified by food habits and these data are summarized in Table 9. It is apparent from this table that the total fish biomass collected on the reef in 1977 is close to that removed in 1966. Most of the biomass in each collection was planktivorous. The relative proportions of herbivore, planktivore, omnivore, and carnivore by biomass were similar for both collections. Table 10 presents a list of the six most abundant fish species by weight collected in 1966. These same species were again the six most important in 1977. The preponderance of biomass in each collection consisted of three planktivorous species (*Abudefduf abdominalis*, *Chaetodon miliaris*, and *Apogon snyderi*). The difference in total biomass recovered in the two collections was about 46 kg. This difference was almost entirely due to a 45 kg decrease in the biomass of *Abudefduf abdominalis* removed in 1977 (51 kg) from that collected in 1966 (97 kg). Other than the herbivorous *Scarus sordidus*, the remaining species of the six most important include *Echidna zebra* and *Gymnothorax undulatus*, which are carnivorous.

Table 11 presents the results of a chi-square contingency test showing that the trophic structure of the fishes on the experimental

Table 9. Trophic structure of the fish community on a patch reef in Kaneohe Bay in 1966 and 1977 based on total removal using rotenone. Values given represent 99% and 98% of the biomasses of fish collected in 1966 and 1977, respectively.

Feeding Category	1966			1977		
	Number of Species	Weight		Number of Species	Weight	
		kg	%		kg	%
Herbivore	10	12.16	7	12	15.63	12
Planktivore	8	116.78	64	8	74.01	55
Omnivore	4	2.02	1	3	2.13	2
Carnivore	48	51.33	28	48	43.40	32
Totals	70	182.29	100	71	135.17	100

Table 10. The six most important fish species by weight in the 1966 and 1977 collections from the experimental reef in Kaneohe Bay.

Species	1966			1977		
	Rank by Weight	Number Collected	Weight kg	Rank by Weight	Number Collected	Weight kg
Abudefduf abdominalis	1	1142	97.0	1	666	50.9
Chaetodon miliaris	2	476	16.7	2	421	18.1
Echidna zebra	3	20	10.5	3	6	4.2
Gymnothorax undulatus	4	66	9.7	4	164	7.6
Apogon snyderi	5	212	5.9	5	123	3.0
Scarus sordidus	6	386	4.5	6	142	3.3
Total		2,302	144.3		1,522	87.1
% of Total Collection		48	78		33	63

Table 11. Values for chi-square contingency tests used in comparing trophic structure stability of the depopulated Kaneohe Bay experimental reef in August 1966, October 1977, and April 1978. The August 1966 and October 1977 data represent complete collection of all fishes; the April 1978 data are based on visual census results. The number of species in each trophic class (upper section) has not changed significantly over time nor has the biomass in each trophic group.

TROPHIC CLASSES BY NO. OF SPECIES

Year	Herbivore	Planktivore	Omnivore	Carnivore	Total
Aug. 1966	10	8	4	48	70
Oct. 1977	12	8	3	48	71
Apr. 1978	10	4	4	15	33
Totals	32	20	11	111	174

χ^2 = 7.72, 6 d.f., P > 0.25

TROPHIC CLASSES BY WEIGHT

Year	Herbivore	Planktivore	Omnivore	Carnivore	Total
Aug. 1966	12.16	116.78	2.02	51.33	182.29
Oct. 1977	15.63	74.01	2.13	43.40	135.17
Totals	27.79	190.79	4.15	94.73	317.46

χ^2 = 3.78, 3 d.f., P > 0.50

reef was not significantly different between the 1966 and 1977 collections both in terms of numbers of species and biomass. Additionally, this trophic structure was re-established within 6 months of the 1977 removal of fishes.

Three algal quadrats erected on the upper slope of the experimental reef showed no obvious changes following fish depopulation. The area was dominated by a single alga, *Dictyosphaeria cavernosa*, whose seasonal growth pattern probably relates to the light regime (Mr. P. Jokiel, personal communication). The herbivorous fishes collected on the experimental reef characteristically fed on fine microalgal filaments growing as epiphytes on *Dictyosphaeria* but do not feed directly on it. Also, the recolonization of herbivorous fish proceeded quickly (see below) and parrotfish attained pre-poisoning population levels within six months of the event (Table 12). Additionally, no changes in the structure of the fish community on the control reef were seen. During each fish census observations were made on the algal and benthic animal community structure and no noticeable changes were seen.

The recolonization of fishes to the experimental reef has been followed up to the present time (October 1978) and Table 12 presents a summary of these data. The curves for colonization and colonization rates for all species (Figure 11) suggest that the MacArthur-Wilson theory of island biogeography may appropriately model these initial stages of recolonization to the experimental reef. As would be expected, the number of species and individuals recolonizing increased with time. The greatest proportion (12 to 92%) of all colonizing individuals were juveniles of the family Scaridae (*Scarus sordidus*,

Table 12. Progression of fish recolonization on a patch reef in Kaneohe Bay, Oahu, following total fish removal by rotenone on 12 October 1977. Day 0 represents fish removed; subsequent data were obtained by visual census.

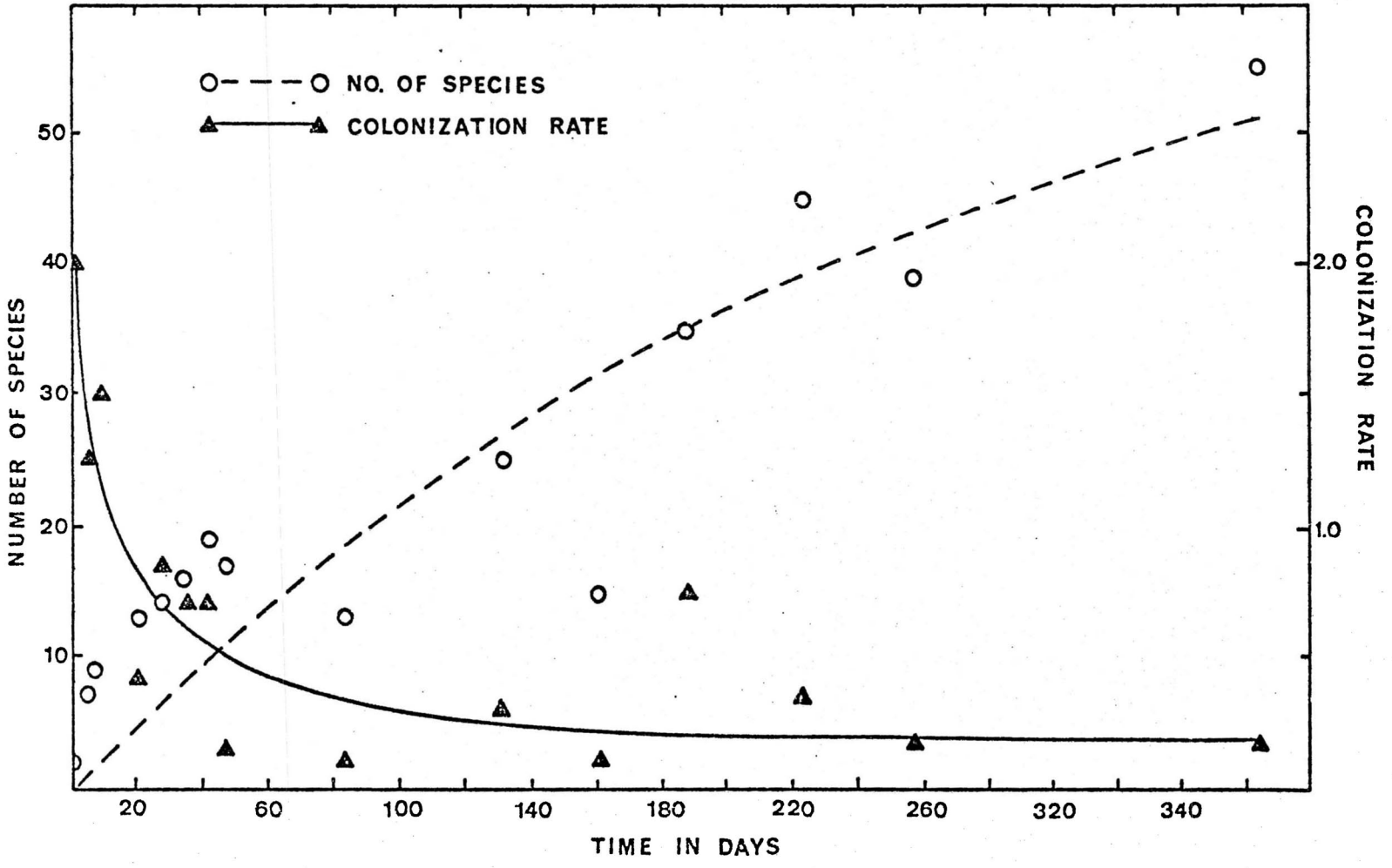
Days After Poisoning:	0	1	5	7	21	28	35	42	49	84	133	161	189	224	258	365
No. of Species	81	2	7	9	13	14	16	19	17	13	25	15	35	45	39	55
No. of New Species	0	2	5	3	7	6	5	5	1	5	17	3	21	13	6	21
No. of Species Lost		0	0	1	3	5	3	2	3	9	5	13	1	3	12	5
Cumulative No. of Species	0	2	7	9	15	19	23	25	26	31	35	37	41	51	55	69
No. of Individuals	4626	23	61	91	219	427	524	442	442	525	624	528	1296	1930	2292	2111
No. of Scaridae	545	21	51	71	201	372	441	314	324	451	395	405	893	1139	1371	1033
% Scaridae	12	91	84	78	92	87	86	71	73	86	61	77	69	59	60	49

Figure 11. The colonization curve (number of species against time) and the colonization rate curve (number of new species divided by the days since the last observation plotted against time) for all fishes recolonizing the Kaneohe Bay experimental reef from 13 October, 1977 to 19 April, 1978. Data are from Table 12. The colonization curve is described by the equation

$$Y = 70\left(1 - e^{-0.0036t}\right)$$

and the colonization rate curve is described by the equation

$$Y = 2.25\,t^{0.43} \quad .$$


NO. OF SPECIES
COLONIZATION RATE
NUMBER OF SPECIES
COLONIZATION RATE
TIME IN DAYS
50
40
30
20
10
2.0
1.0
20
60
100
140
180
220
260
320
340

S. taeniurus, *S. perspicillatus* and *Scarops rubroviolaceus*). Most juveniles were either *Scarus sordidus* or *S. perspicillatus*. Wass (1967) also found Scaridae to be early and the most abundant colonizers during his 241-day study of recolonization on the same reef. In both studies, all of the colonizing Scaridae were juveniles (2-8 cm S.L.). Many of the other fish species recolonizing the reef in 1966 were subadults or adults (Wass 1967); this was the case also in 1977. The large number of juvenile fishes rather than newly metamorphosed individuals recolonizing the experimental reef may be related to the time of reef depopulation relative to normal annual recruitment of Hawaiian fishes. The spring months are the usual time of recruitment for newly metamorphosed individuals of many Hawaiian reef fishes (Miller, Watson, and Leis 1973, Miller 1973).

Discussion

The biomass of fishes collected from the experimental reef in 1966 was calculated to be 1246 kg/ha (Wass 1967); in 1977, 930 kg/ha of fishes were taken. In Hawaii other biomass estimates have been made by Brock (1954); his assessment based on visual transects ranged from 40 kg/ha on sand flats to a high of 1860 kg/ha. In low relief Hawaiian habitats, McVey (1970) found an average standing crop of 106 kg/ha. Other studies on reef fish standing crop utilizing visual methods include the work of Odum and Odum (1955) at Enewetak (425 kg/ha), Clark et al. (1968) 350 kg/ha on fringing reefs in the Red Sea and Bardach (1959) 450 kg/ha on a patch reef in the Caribbean. Wass (1967) compared pre-poisoning visual census data to the results obtained from the poisoning of all fishes on the Kaneohe

Bay experimental reef and found a 42% agreement between the number of fishes that were censused to the number collected. In the present study there was a 59% agreement between those fishes collected and censused. The species "missed" were primarily cryptic in habits.

The above estimates using visual techniques suffer from several observer errors, e.g., failure to see species with secretive or cryptic habits, failure to see species that are wary of the diver, and difficulty in making an accurate assessment of the numbers and sizes of an abundant species. Randall (1963) recognized these shortcomings and used a large net and rotenone to obtain fish standing crop estimates on portions of Virgin Island reefs. For the two collections the average was 1590 kg/ha. Goldman and Talbot (1975) used a dynamite technique in collecting fishes from imprecisely defined areas on the Great Barrier Reef and obtained reef fish biomass estimates from 175 to 1900 kg/ha. These authors concluded from their work and the literature that a reasonable maximum standing crop of coral reef fishes in most communities is probably in the neighborhood of 2000 kg/ha.

Most fish biomass studies have not attempted to break the total standing crop down into component trophic levels below the level of herbivore, omnivore and carnivore. Odum and Odum (1955) found that herbivores were more important than carnivores on a weight basis. In contrast, other studies (Hiatt and Strasburg 1960, Al-Hussaini 1947, Randall 1963, 1967; Talbot 1965, Bakus 1969, Talbot and Goldman 1972, Goldman and Talbot 1975) found that carnivorous fishes are the single most important trophic level by weight. This reversal of the traditional biomass pyramid results from opportunistic

carnivorous fishes feeding on second and third trophic level invertebrates (Goldman and Talbot 1975). Only by considering the trophic structure of the entire reef will the true biomass picture become clear.

Only one study of reef fish biomass (Goldman and Talbot 1975) presented a detailed breakdown by trophic group in which Great Barrier Reef planktivores comprised 12% of the fish biomass. The biomass figures for the Kaneohe Bay experimental reef heavily favor planktivores and carnivores. In the present study planktivorous fishes dominated the experimental reef (55% by weight) as they did in the 1966 study (64%). This is due to the large standing crop of *Abudefduf abdominalis* and *Chaetodon miliaris* in both collections. Herbivorous and/or omnivorous species comprised a small proportion of the standing crop by weight (Table 9). In other Hawaiian habitats, planktivorous fishes usually make up a small percentage (10-15%) of the standing crop (R. Brock, unpublished data). The data from the experimental reef suggest that Kaneohe Bay must support a larger than usual zooplankton community. Ongoing zooplankton research both in Kaneohe Bay and in other Hawaiian nearshore habitats support this contention (W. Kimmerer, pers. comm.).

Only 40% of the species taken in the 1974 depopulation of fish from the Kaneohe Bay experimental reef are in common with those removed in 1966. This lack of taxonomic persistence may be explained by (1) a change in the habitat from 1966 to 1977 making it unacceptable to some species; (2) chance colonization (Russell et al. 1974, Sale and Dybdahl 1975, Smith 1977, Sale 1978); (3) order of species settlement, i.e., those species arriving early determine the fate of

later arrivals through competitive superiority (Nolan 1975); (4) species composition determined solely by the species pool locally available; (5) colonization dependent upon the time of fish removal or (6) some combination of these factors (C.L. Smith 1978).

Environmental degradation has proceeded on patch reefs of Kaneohe Bay for many decades (Daveney et al. 1976) and has continued since the 1966 fish removal. The near absence of crustacean and zooplankton-feeding groups such as the holocentrids and priacanthids common in the 1966 collection but rare in 1977 indicates the loss of shelter under coral heads. Members of these two families normally seek shelter during daylight hours (Gosline and Brock 1960, Hobson 1974). Today much of this coral shelter habitat has been covered by the alga *Dictyosphaeria cavernosa* (see Chapter 2). However, the relationship between environmental degradation and the species richness on the experimental reef is not readily apparent; even with the loss of habitat space the standing crop of fishes in both the 1966 and 1977 collections are similar (Table 9). Also, five more fish species were taken in 1977 than in 1966.

Reef fishes are highly specialized and the adaptive value of these specializations may be as mechanisms for resource sharing which allow greater species packing. On inspection coral reefs appear to be densely populated and most surfaces and the water column above them are occupied; this suggests that space may be a major limiting resource (Sale and Dybdahl 1975, Sale 1978, C.L. Smith 1977, 1978). Many fish species show a considerable overlap in their food requirements (Jones 1968*a*) thus de-emphasizing this resource. A primary use of space is for shelter, implying that many coral reef fishes may

be predator limited (C.L. Smith 1977). Experimental evidence supporting this concept comes from the work of Nolan (1975) who removed piscivore predator species and caged a small patch reef. This resulted in an increase in resident fish species diversity. However, if space is an important resource to fishes, it is not partitioned by some of them on the basis of precise microhabitat requirements. Sale and Dybdahl (1975) in a study of repeated defaunations and colonizations of small patches of reef on the Great Barrier Reef, found different assemblages of fishes recruiting to their experimental reefs. They reasoned that if strict microhabitat requirements (e.g., space) were important to the species involved, colonization should have been by the same species as were there previously. These authors concluded that chance factors were responsible in determining the outcome of colonization (summarized in Sale 1978). Russell et al. (1974) following recruitment and colonization on artificial reefs on the Great Barrier Reef reached the same conclusion, and they noted that the physical structure of their artificial reef habitats were relatively unimportant in determining the community structure during early colonization. Nolan (1975) found no obvious correlation between reef substratum complexity and fish species diversity on artificial reefs erected in the lagoon at Enewetak Atoll.

At 365 days following the 1977 depopulation there were 55 fish species present on the Kaneohe Bay experimental reef, fifteen (27%) of which were not taken in the collection. At approximately 200 days after the 1966 removal of fishes there were 37 species of present and five (or 14%) of these were not on the reef at the time of depopulation (Wass 1967). These data suggest a certain degree of taxonomic

stability present in the system. Perhaps the majority of the fish species initially colonize the experimental reef through some mechanisms other than "chance factors." At 365 days, colonization appears to be incomplete relative to the number of species present in both the 1966 and 1977 collections.

Nolan (1975) at Enewetak found that colonizing fish communities reach an equilibrium after 100 to 200 days that is essentially indistinguishable from the background fluctuation seen on control reefs. His reefs were considerably smaller (one order of magnitude less in volume) than the Kaneohe Bay experimental reef. Being smaller, these reefs may attain a species equilibrium more quickly than a larger reef. Additionally if the site chosen for the colonization study is small relative to the home ranges of some of the fish species residing nearby, depopulation and subsequent colonization studies may yield biased results if the territorial limits of the adjacent residents expand to incorporate the open habitat. Chance factors are probably important determinants of structure at some point below the community level for some species, but at the community level there is some persistence and hence predictability among many fish species colonizing the experimental reef.

The fishes of the experimental reef have maintained a stable trophic structure. The chi-square contingency test on the data presented in Appendix Table XV and Table 9, suggests that there was no significant changes in the trophic structure of the community collected in August 1966 and October 1977 (Table 11). Additionally, by April 1978 the trophic structure of fishes existing on the reef in October 1977 was re-established. Also, the standing crop of fishes

in each trophic class did not significantly change between the two removals (August 1966 and October 1977).

Using Wilson and Simberloff's (1969) data from defaunated red mangrove islands, Heatwole and Levins (1972) found that the non-aquatic invertebrate trophic structure of these islands re-establishes similarly without a concurrent re-establishment of taxonomic structure.

Insular recolonization has received considerable attention in both theory and application following the formulation of a quantitative theory of island biogeography by MacArthur and Wilson (1967). The theory is based on the concept of a dynamic equilibrium between immigration and extinction of species on islands. Experimental evidence supporting the theory abound to such an extent that Simberloff (1976, p. 572) noted

> "the...theory [is] so widely accepted as an accurate description of nature that failure of an experiment to yield the result deduced from the theory leads not to rejection of the theory but rather to attempts to fault the deductive logic or experimental procedure, or simply to willful suspension of belief in the experimental result."

Determination of insular colonization and extinction rates and curves have been calculated for birds (Diamond 1969, 1971), insects (Wilson and Simberloff 1969, Simberloff and Wilson 1969, 1970; Simberloff 1969, 1976), protozoans (Cairns et al. 1969), benthic marine organisms (A. Schoener 1974*a*, 1974*b*; Fager 1971) and marine fishes (Nolan 1975).

In the present study depopulation of the Kaneohe Bay experimental reef has lead to a colonization curve (number of species present against time) for marine fishes that in initial colonization may be described by the asymptotic growth function, e.g.,

$\hat{Y} = 70\left(1 - e^{-0.0036t}\right)$ where Y = the number of species and t is time in days. Logarithmic transformation of these data yield a coefficient determination (r^2) of 0.92; the curve is presented in Figure 11. The colonization rate curve is also depicted in this figure. The colonization rate as defined by Cairns et al. (1969) is the number of new species present at the end of an observation period divided by the time interval between census periods. For the initial recolonization of the experimental reef by fish this curve is best described by the exponential, $\hat{Y} = 2.25t^{0.43}$ where Y equals the colonization rate and t is time in days. Logarithmic transformation of these data provides a coefficient of determination (r^2) of 0.87.

Decolonization or extinction rate is defined as the number of species lost at the end of a census period divided by the length of that time interval (Simberloff 1969, Cairns et al. 1969, A. Schoener 1974*a*). This rate plotted against time yields an extinction-rate curve. During early colonization (the non-interactive period of colonization of MacArthur and Wilson 1967) this curve should be a monotonically increasing function, meaning as more species colonize an empty habitat (island), there is an increasingly greater chance of an extinction occurring until an asymptote is reached. Calculation of the extinction rate from data presented in Table 12 for fishes invading the experimental reef resulted in a negative exponential curve whose slope differed significantly from zero ($P > 0.05$). Thus as more fish species invaded the experimental reef with time, the extinction rate decreased. This contradiction to the theory may be related to (a) the relatively small size of the experimental reef; (b) due to observer errors during censuses; (c) due to species interactions; or (d) related to

unrecorded events.

An attribute of a small reef is that it may harbor proportionately fewer individuals of a species than a larger reef. Thus any factor causing extinction (such as predation, competition, or natural aging) will have a greater impact on the community and be more quickly evident on a small reef than on a larger one. Perhaps the Kaneohe Bay experimental reef is too small to enable accurate estimates of extinction. Observer errors such as missed species due to cryptic habits or low water transparency may have profound effects on both calculated extinction and colonization rates. The inability of the observer to differentiate wandering species could also affect the curves but such species on the experimental reef are rare. Another possibility for the decreasing extinction rate curve may be related to the combination of fish species accumulating with time (as in "assortative" equilibrium--Wilson 1969) that are favorable for the survival of certain immigrant species. Lastly, a problem for both colonization and extinction rate curves recognized by A. Schoener (1974*a*) is that unrecorded events between censuses may not only alter curves but can completely reverse their slopes, thus their validity may be questionable.

From a taxonomic standpoint, the parrotfishes (Scaridae) may be the single largest family by weight on many tropical reefs. This has been substantiated in the Caribbean (Randall 1963). The Scaridae are also important on Marshall Island reefs (Bakus 1967), on the Great Barrier Reef (Goldman and Talbot 1975), at Guam (Jones and Chase 1975) in Hawaii (V. Brock 1954, R. Brock, unpublished data) and at Johnston Atoll (present study). On the Kaneohe Bay

experimental reef the Scaridae comprised only 5% of the standing crop in 1966 and 8% of the biomass in 1977.

The Scaridae are one of the most successful groups of fishes to re-establish and persist on the experimental reef to date (Table 12). Once the removal of fishes had been completed, scarids made their reappearance on the experimental reef very quickly. Parrotfishes rapidly increased in numbers to an estimated maximum of about 1400 individuals approximately 260 days after poisoning; sometime after this, they decreased in numbers probably in response to predation and competitive interactions. It is unknown how quickly the scarid population of the experimental reef will attain a numerical abundance similar to that present prior to poisoning, but the time will at least exceed one year.

By family, parrotfish were the major component of fish recolonization both in numbers and biomass on the experimental reef in 1977. The majority of the scarids colonizing were juveniles (3 to 8 cm S.L. probably in their first year of life). In contrast, McVey (1970) followed the colonization of fishes to an artificial reef in deeper Hawaiian waters (12-33 m) and found that of 11 common species colonizing within the first few months only three were resident *Adioryx xantherythrus*, *Dascyllus albisella* and a herbivore, *Zebrasoma flavescens*. Wass (1967) found juvenile scarids to predominate in the colonization of the Kaneohe Bay experimental reef for the duration of his study (241 days after defaunation). The rapid appearance of parrotfish after the 1977 defaunation did not allow me to answer the question of what happens to a coral reef in the absence of rasping and grazing fishes. The colonization evidence suggests

that scarids are opportunistic in their habitat selection and that schools of juveniles may travel long distances. Bardach (1959) and Ogden and Buckman (1973) found that parrotfish roam over substantial portions of reefs as well as between reefs. It is not known if the parrotfishes continuing to colonize the experimental reef remain permanently on the reef. It may be that the normal colonization of juvenile parrotfish requires them to continually move over large areas of reef until a habitat is found harboring scarids in numbers below some critical density. Alternatively, the home range of parrotfishes (if it applies) may encompass several patch reefs in Kaneohe Bay.

The question of the validity and accuracy of the visual census method is difficult to assess. Judgement of what species are cryptic or wary of divers and would not be censused accurately but taken in a subsequent poison station should be made. V. Brock (1954), Wass (1967), McVey (1970), Jones and Chase (1975), Jones and Thompson (1978), and Russell et al. (1978) have discussed the problem. Rather than attempt a detailed assessment, I will restrict my discussion to the diurnally active and ubiquitous Scaridae.

The small scarids characteristic of the Kaneohe Bay experimental reef have a tendency to hover in an area near the crest of the reef when a diver is nearby. One day prior to the defaunation I carried out a series of three 4 × 20 m visual transects all of which in some part of their length crossed the crest or edge of the reef. In total, 188 parrotfishes were censused. I made the assumption that at the time of counting, the parrotfish were restricted to an area extending on the reef flat no more than 4.6 m (15 ft.) nor extending seaward of the reef crest no further than 4.6 m. This represents a planar

area of 736 square meters; the transects sampled 240 square meters. An estimate of the number of parrotfish on the reef may be obtained:

$$\frac{736}{240} \times 188 = 577 \text{ fish.}$$

In the depopulation 545 parrotfishes were collected. Considering the difficulty of making an accurate census of such an abundant fish, I think that these results point out the validity of the visual census technique, bearing in mind other shortcomings and pitfalls in the method. The technique is probably equally valid for other diurnally active reef fish species.

CHAPTER 9

THE RELATIONSHIP OF PARROTFISHES TO CORAL REEFS AND TO MAN

The Effects of Parrotfishes on the Coral Reef Community

Parrotfishes are one of the most important families of fishes by numbers and weight on many coral reefs including those in the Caribbean (Randall 1963), in Kaneohe Bay (Chapter 8), Johnston Atoll (Chapter 5), and on many Pacific reefs (Bakus 1967, Goldman and Talbot 1975, Jones and Chase 1975). In the coral reef environment, parrotfishes appear to favor areas that have a considerable amount of open hard substratum adjacent to high cover that serves as shelter. Juveniles of the Hawaiian species often form mixed schools which may range from a few to more than 1500 individuals. Adult *Scarus sordidus* females and subadult female *S. perspicillatus* will often travel with these schools of juveniles. One adaptive advantage of forming such schools lies in the ability of these grazers as a group to overrun and feed in the defended territories of other resident reef fishes (Low 1971). Adults of all *Scarus* species may form small, mixed aggregations but adult terminal male *S. sordidus*, *S. perspicillatus*, *S. dubius* and *Calotomus sandvicensis* of all sizes are usually solitary in their habits.

The analyses of gut contents suggests that Hawaiian parrotfishes may be separated into two groups, those that feed primarily on epilithic communities (*Calotomus sandvicensis*, *Scarus dubius*) and

those that feed not only on these benthic surface communities but also on the cryptobiota present within the coralline substratum, as suggested by the consistently greater proportion of calcium carbonate in their gut contents. The jaw structure (mandibles) of these latter species (*Scarus sordidus, S. perspicillatus, S. taeniurus*) is much heavier; the ratio of the standard length divided by the jaw weight supports the gut content data. Species possessing heavy jaws have a ratio of 70 mm/g or less and light-jawed species have a ratio of 150 mm/g or more. The scarids feeding only on epilithon probably compete more directly with other herbivorous fishes (e.g., acanthurids) for available algal resources than do the parrotfishes that rasp deeply into the coralline substratum for their food. Previous studies have however found considerable overlap in the use of food resources by herbivorous coral reef fish species (Jones 1968).

Field evidence suggests that if these rasping fishes feed on surface communities only, they may drastically effect the benthic community structure and biomass; in a three-dimensional system (normal coralline substrata) their effects as manifested through their feeding are much less severe, but they may cause the diversity of benthic species to increase. These data are few and hence not statistically conclusive. On the other hand, laboratory experiments indicate that low densities of parrotfishes cause benthic community structure to proceed to macroalgal dominance; at intermediate levels of grazing intensity (0.6 to 1.5 fish/m^2 or 9 to 17 g wet weight/m^2) a diverse community develops which is enhanced by the presence of spatial refuges (a third dimension). Likewise the growth of parrotfish is greatest at these densities. At densities greater than 1.9 fish

or 20 g wet weight/m^2 and in the absence of refuges the resultant benthic community is of low diversity and biomass. Experimental optimum densities of parrotfishes are similar to observed field densities in Kaneohe Bay, Oahu.

Parrotfishes are not the only contributors to change in benthic community structure through their feeding activities; sea urchins have also been implicated (Paine and Vadas 1969, Dart 1972, Ogden et al. 1973, Krumbein and Van der Pers 1974, Schuhmacher 1974, Estes and Palmisano 1974, Sammarco et al. 1974, Bak and Van Eys 1975, Benayahn and Loya 1977, Stearn and Scoffin 1977, Ogden and Lobel 1978). The evidence presented in this study suggests that parrotfishes alone may effect the benthic community structure (microcosm experiments, Chapter 7). Sea urchins were rare or absent on the patch reefs in Kaneohe Bay but parrotfishes were abundant. As noted above, the number of parrotfishes resulting in optimum benthic community development (diversity and biomass) in the laboratory experiments were similar to observed Kaneohe Bay field densities. In this situation, the standing crop of cryptobiota (a potential food resource) average from 50 to 70 g dry weight/m^2. At the Johnston Atoll study site where sea urchins were as abundant as parrotfishes (Chapter 5) the mean biomass of the cryptobiotic component was about 9 to 10 g dry weight/m^2. This low biomass most probably was the result of physical disturbance to the substratum (rock turnover) and intense grazing pressure by both parrotfishes and sea urchins. The low cryptobiotic biomass figures suggest that the benthic community in the vicinity of the Johnston Atoll study site (windward reef rubble zone) was probably receiving near maximum sustainable utilization by

grazers, however, their effect on the diversity of benthic species was not a negative one.

The Impact of Man on Parrotfish

Some reef fish species apparently are specific in their habitat requirements. Thus a small change in a coral reef community due to an environmental stress may result in the loss of certain fish and invertebrate species. Many of the man-induced environmental perturbations in Hawaiian reef systems have not lead to the local disappearance of parrotfishes. Indeed, simple removal of all fishes from a patch reef is followed rapidly with colonization by parrotfishes in large numbers (Chapter 8). Their success in such recolonization probably is related to wide patterns of movement of both juveniles and adults. However, extreme fishing activity, changes in the substratum resulting in the loss of appropriate food resources or the reduction of available cover may cause local loss of parrotfishes.

Drastic habitat changes may lead to the local near disappearance of parrotfishes. The southeastern part of Kaneohe Bay serves as one example. The water in this area is characterized by a high particulate and nutrient load (Chapter 2) and has few parrotfishes. Fish transects conducted over similar selected reef crests during a two year period resulted in a mean of 0.1 parrotfish/m^2 in the southeastern sector and 1.0 parrotfish/m^2 in the central bay sector. The hard substratum in the southeastern sector was dominated by large filter feeding forms (barnacles, etc.) such that appropriate parrotfish food resources (microalgal, cryptofaunal and coralline) were probably lacking. Fishes found in this habitat were primarily planktivores or

detritivores.

Other reef areas receiving drastic habitat changes are those fronting Waikiki Beach. Prior to 1951 the substratum off Waikiki was a composite of hard bottom, rubble, sand, and live corals (see Edmondson 1928). Over the years sand was brought in to improve the beaches of Waikiki. Much of this sand has been carried offshore by currents, burying the hard substratum; this was coupled with increased runoff from hinterland urbanization leading to a decrease in the abundance of live corals on many Waikiki reefs (personal observations). Parrotfishes as well as many other reef fishes are nearly absent from this system. Most of the remaining hard substratum in water less than 12 m in depth is dominated by large fleshy algae where scouring by sand is not too great. In general, pristine Hawaiian reef areas surveyed both casually and quantitatively by the author over the last 28 years do not have a preponderance of large fleshy algal species. Rather, the algae present are either coralline (encrusting) forms or very small in size. Invariably such systems have numerous parrotfishes.

Intense fishing activity may appreciably reduce resident parrotfish stocks. The probable result of such fishing pressure may be seen on the reefs in the vicinity of Moen Island harbor (Truk Atoll). This area, surveyed by the author from shore to depths of 25 m in 1975, includes much hard substratum with live coral and large areas of macroalgae (*Padina, Lyngbya, Dictyopteris, Sargassum*). The large standing crop of benthic algae is unusual in such atoll situations; its presence may be related to the relative rarity of parrotfishes and other herbivorous species. Fishes were very scarce in transects and

those present were mostly juveniles. Although illegal, fishing by use of explosives was once commonplace and I believe it still occurs in the lagoon. Evidence of this type of fishing was seen (large areas to 100 m^2 in area where the corals had been recently broken apart). It is probable that the shock wave associated with this kind of fishing kills fishes in a radius much greater than that of the visible coral damage (Russell et al. 1978). Such fishing may be totally disruptive to the reef community.

Parrotfishes are taken in the Hawaiian Islands by net and spear. Adult scarids rarely enter traps and their presence in the inshore commercial net fishery is incidental. The mean annual Hawaiian commercial catch has decreased in recent years. During the period from 1947 to 1957 the catch of parrotfishes averaged 5090 kg annually; in the 1957 to 1967 period it was 3140 kg per year and from 1967 to 1977 it averaged only 2090 kg per year (mimeo leaflet from Department of Land and Natural Resources, State of Hawaii). These catches probably have a trivial impact on local parrotfish populations. The decline in the catch of parrotfishes more likely is related to a decline in the number of boats and fishermen engaged in inshore fisheries about the islands in recent years and possibly to the degradation of their habitat.

The primary fishery for parrotfishes is recreational in Hawaii where they are sought after by both net and spear fishermen. No assessment of this fishery has been made in this study but a substantial number of parrotfishes must be taken annually. They are particularly susceptible to spearfishing methods at night when asleep in the coral. This may be contrasted to Johnston Atoll where the

removal of fish is almost nil (personal observation).

Besides the mortality due to fishing, predation on parrotfishes is another aspect not addressed in this study. Parrotfishes appear to be an important prey for many large piscivorous carnivores. Brock (1972) found that parrotfishes were the most common family of reef fishes consumed by large eels (*Gymnothorax javanicus*) at Johnston Atoll. Because quantitative information on recruitment, growth and mortality is lacking the parrotfish resource in Hawaiian reefs cannot now be managed. Management of this resource should be considered, for evidence presented in this study suggests that parrotfishes are important agents in structuring the coral reef community in which they live.

CHAPTER 10

SUMMARY

1. Both field and laboratory observations suggested that rasping parrotfishes (Family Scaridae) do affect the structure of the benthic community through their feeding activities.

2. Average densities of parrotfishes in the field appreciably altered the benthic community structure in two-dimensional systems (e.g., settlement plates). On natural substratum (coral rubble) parrotfish feeding caused an increase in the diversity of benthic organisms present. The addition of a third dimension (substratum interior space) appeared to alleviate the otherwise negative impact of feeding on community structure. It is postulated that the benthic community present on and in coralline substrata at the Johnston Atoll study site evolved its maximum organism diversity under this herbivore influence. Additionally, the presence of a third dimension has given the epibiota and cryptobiota the resilience necessary to survive through provision of refuges.

3. Gut content studies demonstrated that parrotfishes consume large amounts of calcium carbonate (collectively, about 65% by volume). In the Hawaiian faunal region parrotfishes rarely fed on live corals. Rather, those species with relatively heavy dentition (*Scarus sordidus*, *S. perspicillatus* and *S. taeniurus*) took in relatively more calcium carbonate (limestone) and probably cryptobiota than did species with structurally lighter jaws (*Scarus dubius* and *Calotomus sandvicensis*). The latter species appeared to feed more on benthic surface materials.

Probably not much energy is derived on a per unit time basis by parrotfishes feeding on coralline substratum, inasmuch as they spend approximately 60% of the daylight hours actually feeding. Laboratory experiments showed that small parrotfish (*Scarus sordidus* and *S. taeniurus*) consumed surface microalgal resources (measured by chlorophyll-*a* extraction) at a rate of 4.9 to 9 µg chlorophyll-*a* per gram (wet weight) of parrotfish per day. The standing crop was about 7 µg chlorophyll-*a* per cm^2 of coralline surface. Few other fishes found on coral reefs are capable of directly utilizing as food the cryptobiota in coral rock.

4. Experiments conducted in a flow-through microcosm system demonstrated that parrotfish growth (weight gain) was greatest at densities of fish similar to those observed in the field (0.6 to 1.5 fish/m^2 or 9 to 17 g wet weight of fish/m^2). At parrotfish densities below this level microalgal species dominated the exposed benthic community and above these levels this community was less diverse and of lower biomass with calcareous algal species being favored. The addition of refuges to such a system resulted in the occurrence of a greater benthic species richness and biomass. Refuges provided increased habitat heterogeneity affording greater protection for benthic species from the grazing parrotfish. As parrotfish grazing pressure increased, the benthic species richness and biomass increased in both exposed and refuge habitats up to moderate levels of predation (similar to field densities). These data support the contention that in structurally simple environments predation first increases then decreases species diversity as it increases in intensity. However, coral recruitment, like coralline algae, was enhanced by

increased grazing pressure above these intermediate levels (and by refuges). Newly settled corals escape predation by grazing parrotfishes through initial rapid growth to a size that small parrotfishes will avoid. Coral and coralline algae produce important lithological components of modern coral reefs; evidence presented in these laboratory experiments suggests that parrotfish may be important to the success of these structural elements and thus may be serving as a keystone species for benthic community development.

5. Depopulation and recolonization studies conducted on an isolated patch reef suggest that the recolonizing of the reef by fishes follows the MacArthur-Wilson model of insular colonization. The standing crop of fishes removed from the reef amounted to 930 kg/ha. In a collection made 11 years previously, the same reef yielded 1230 kg/ha. The trophic structure of the fish community was similar 11 years later and within 6 months of fish depopulation had returned to an equilibrium condition. Planktivorous species dominated the community (in 1977, 55% by weight) followed by carnivores (32%), herbivores (12%) and omnivores (2%). In most reef systems, carnivores are the most abundant fishes; the large standing crop of planktivores was related to local nutrient enrichment. Twelve percent of the numbers and 8% of the wet biomass of fishes from the reef in 1977 consisted of parrotfishes. These values were low relative to other studies which provide evidence that parrotfishes are a dominant family on many reefs by numbers and weight. However, over the course of fish recolonization reported here (12 months) parrotfishes were one of the most abundant and successful recolonizing groups (69% of all individuals), suggesting that they are opportunistic in their habitat selection.

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Appendix Table I. Results of observations on the settlement plate experiment conducted at the Johnston Atoli study site. The October 1975 plates were immersed for 5 months, the April 1976 plates for 6 months. The numbers in the columns represent the number of individuals by species for each of three treatments, i.e., exposed to grazing, exposed to grazing but under a roof (shading effect) and not exposed to grazing (caged). A check in a column indicates presence or absence of certain colonial forms. The Shannon-Weaver Index of diversity (H') and total dry weight of both plants and animals are given in Table 1 of the text.

	OCTOBER 1975			APRIL 1976		
TAXONOMIC GROUP	Exposed	Caged	Under Roof	Exposed	Caged	Under Roof
Phylum Cyanophyta						
sp. 1 (probably *Schizothrix*)		✓			✓	
sp. 2	✓	✓	✓	✓	✓	✓
sp. 3			✓			✓
Phylum Rhodophyta						
encrusting calcareous sp. 1	✓	✓	✓	✓	✓	✓
sp. 2	✓		✓	✓		✓
Jania sp.					✓	
Phylum Protozoa						
Class Rhizopodea						
Triloclina sp.		7			1	
Amphistigina sp.		11		1	145	25
Phylum Platyhelminthes						
Class Turbellaria						
O. Acoela						
sp. 1					1	
Phylum Nemertina						
sp. 1					1	
Phylum Nematoda						
sp. 1					19	
sp. 2					18	
Phylum Sipuncula						
Aspidosiphondae sp. 1		2			1	

Appendix Table I. (continued)

TAXONOMIC GROUP	OCTOBER 1975			APRIL 1976		
	Exposed	Caged	Under Roof	Exposed	Caged	Under Roof
Phylum Mollusca						
Class Gastropoda						
Conus sp. (juvenile)					2	
Cerithium sp. (juvenile)					1	
micromollusca sp. 1					9	
sp. 2					7	3
sp. 3						4
sp. 4		2			2	
sp. 5						1
sp. 6						1
sp. 7					1	
Nudibranch sp.					9	
Phylum Annelida						
Family Syllidae sp. 1		1				
sp. 2		4			10	
sp. 3		1			1	
sp. 4		1			2	
Trypanosyllis zebra					1	
Exogoninae sp. 1		7		1	6	
Sphaerosyllis sp.		2				
Eunice afra punctata					1	
Lumbrineris unicornis					1	
Family Lumbrineridae sp. 1		1				
Family Dorvilleidae sp. 1		1				
sp. 2		2				
Polyophthalmus pictus		2			3	
Family Opheliidae sp. 1		3			1	
sp. 2					1	
Family Palmyridae sp. 1					3	
Family Polynoidae sp. 1		2				
Family Spionidae sp. 1					15	
sp. 2		2			43	2
sp. 3					3	
Family Capitellidae sp. 1					1	
Mesochaetopteous sagitarrius					1	
Family Cirratulidae sp. 1		54				
sp. 2		2				
Pileolaria koehleri	12					
Janua sp.	4					
Spirorbinae sp. 1 (dextral)						1
Phylum Arthropoda						
Class Crustacea						
Subclass Copepoda						
sp. 1					2	1
sp. 2					33	1
sp. 3						

Appendix Table I. (continued)

TAXONOMIC GROUP	OCTOBER 1975			APRIL 1976		
	Exposed	Caged	Under Roof	Exposed	Caged	Under Roof
sp. 4					1	
sp. 5					1	
Subclass Malacostraca						
O. Tanaidacea		3				
sp. 1					7	1
O. Isopoda						
sp. 1					1	1
sp. 2					1	
sp. 3		1			1	
O. Amphipoda						
Gammaridea						
sp. 1		1				
sp. 2		1			7	1
Caprellidea						
sp. 1					50	
sp. 2					1	
O. Decapoda						
Palaemon sp.					2	
Section Brachyura						
crab megalops		1			6	
Phylum Bryzoa						
Bryozoa encrusting sp. 1	1	3	3			
Phylum Echinodermata						
Class Asteroidea						
Linkia sp.					1	
Class Holothuroidea						
Holothuria sp.					1	
SUMMARY:						
Total Number of Species	6	30	5	7	51	12
Total Number of Individuals	17	125	3	4	429	40

Appendix Table II. Taxonomic groups of organisms found in calcium carbonate rubble substratum samples from two treatments exposed to grazing (control), and not exposed to grazing (caged). The caged samples were removed from cage number 1 in the Johnston Atoll study area; all exposed samples were taken within 30 cm of the cage on the dates as indicated. Physical characteristics of each sample are given in Table 2. Crustacean identifications were made by Mr. W. Cooke, University of Hawaii.

TAXONOMIC GROUP	SAMPLE DATE						
	May 1975 Exposed	Aug. 1975 Caged	Aug. 1975 Exposed	Oct. 1975 Caged	Oct. 1975 Exposed	Apr. 1976 Caged	Apr. 1976 Exposed
Algae	✓	✓	✓	✓	✓	✓	✓
Phylum Protozoa							
Class Rhizopodea							
Foraminifera spp.	50	26	30	20	89	23	406
Phylum Porifera							
Class Demospongia							
Cliona sp.	✓		✓	✓			✓
Phylum Cnidaria							
Class Anthozoa							
O. Actiniaria sp. 1	1		1	11	4	3	11
O. Madreporaria sp. 1							✓
Class Hydrozoa							
Hydrozoan spp.			✓	✓	✓	✓	✓
Phylum Platyhelminthes							
Class Turbellaria							
Polyclad sp. 1	1					1	
Phylum Nemertina							
Nemertine spp.			3	8	7	7	7
Phylum Nematoda							
Nematode spp.	12	21	105	51		47	119
Phylum Entoprocta							
Entoprocta sp. 1					1		
Phylum Sipuncula							
Sipunculan spp.	5	26	53	24	48	34	438
Phylum Mollusca							
Class Scaphopoda							
Scaphopod sp. 1		2					

Appendix Table II. (continued)

TAXONOMIC GROUP	SAMPLE DATE: May 1975 Exposed	Aug. 1975 Caged	Aug. 1975 Exposed	Oct. 1975 Caged	Oct. 1975 Exposed	Apr. 1975 Caged	Apr. 1975 Exposed
Class Bivalvia							
Bivalve spp.		1	3	3	1		1
Class Gastropoda							
Gastropod spp.	4		6	12		15	3
Phylum Annelida							
Class Polychaeta							
Family Aphroditidae				1	1		1
Family Palmyridae		1	1	5		2	1
Family Amphinomidae	17	24	9	30	4	15	14
Family Phyllodocidae	4	1	11		4	3	4
Family Hesionidae			2				
Family Syllidae	58	138	334	277	100	139	398
Family Nereidae				2		2	
Family Glyceridae	1	3	2	1		1	1
Family Euncidae	12	37	29	82	86	83	490
Family Lumbrineridae				13			
Family Dorvilleidae	1	1	26	14	3	5	19
Family Spionidae	145	10	65	369	25	222	471
Family Cirratulidae	4	2	15	30	51	16	171
Family Chaetopteridae				3			
Family Paraonidae		1	1	1		6	22
Family Pheliidae			3	4	1		1
Family Capitellidae		7	15	7	3	13	14
Family Terebellidae		1	2			1	1
Family Sabellidae	1	9	34	30	13	12	32
Family Serpulidae	1		12	17	2	2	3
Unidentified Sedentaria		1				1	14
Phylum Bryozoa							
Bryozoa sp. 1	✓			✓	✓		✓
Phylum Echinodermata							
Class Ophiuroidea							
Ophiuroid sp. 1				3			
Phylum Arthropoda							
Class Pycnogonida							
Pycnogonid sp. 1				1			
Pigrogromitus timsanus							1
Class Crustacea							
Subclass Copepoda							
Copepod spp.	1		7	9		2	6
Subclass Cirripidia							
O. Acrothoracica							
Barnacle spp.	16		6	12	2	10	21

Appendix Table II. (continued)

TAXONOMIC GROUP	SAMPLE DATE						
	May 1975 Exposed	Aug. 1975 Caged	Aug. 1975 Exposed	Oct. 1975 Caged	Oct. 1975 Exposed	Apr. 1976 Caged	Apr. 1976 Exposed
Subclass Malacostraca							
O. Cumacea							
sp. 1			2	4			
O. Tanaidacea							
Lepthochelia sp. 1	4	1	14	15		3	2
Apseudes sp. 1			3			5	
sp. 2			1	4			
sp. 3	2			102			
Pagurapseudes sp. 1				13			
O. Isopoda							
Family Janiridae sp. 1	2		2	1		1	2
sp. 2	1		7	7			
Family Gnathidae							
sp. 1	1		3	13	1		1
Family Gnathidae							
sp. 2			1	8			
Family Anthuridae							
sp. 1	63	3	2	44	17	4	12
Family Anthuridae							
sp. 2	1					2	
Family Sphaeromatidae							
sp. 1				8	1		3
Family Corallanidae							
sp. 1							1
O. Amphipoda							
Family Caprellidae							
sp. 1	5		1	1			
Elasmopus sp.	4			2	1		
Amphithoe sp.	3						
Lembos sp. 1	2		4	11		3	
sp. 2							
Leucothoe sp. 1				5	2		
sp. 2				2			
Podocerus sp. 1					1		
Ceradocus hawaiiensis				2			
Family Amphithoidae							
sp. 1					1	1	3
Family Amphilochidae							
sp. 1				1			2
Family Photidae sp. 1				2			
Maera sp. 1						1	
sp. 2						2	
Amphipoda unident.	6						
O. Decapoda							
Suborder Natantia							
Alpheus sp. 1			1	1	1		
sp. 2				2			
sp. 3				1			
larval shrimp sp.1			1				
Suborder Reptantia							
Hermit crab sp.					1	1	2

Appendix Table II. (continued)

TAXONOMIC GROUP	SAMPLE DATE: May 1975 Exposed	Aug. 1975 Caged	Aug. 1975 Exposed	Oct. 1975 Caged	Oct. 1975 Exposed	Apr. 1976 Caged	Apr. 1976 Exposed
Section Brachyura							
Family Portunidae sp. 1	1			3	4		1
Family Maiidae sp. 1				1			
Family Xanthidae sp. 1	1			1			
sp. 2			1	1	1	1	
sp. 3	3		2	16		2	8
sp. 4					1		
sp. 5					1		
sp. 6	1	2			17		
Megalops sp.						1	1
Unknown "white worms"?		37	53	7	75	11	69
SUMMARY:							
Number of identifiable taxa	37	24	44	60	37	41	45
Number of Phyla	11	7	10	12	10	10	11
Number of Polychaete families	10	13	16	17	12	15	16
Number of Crustacean species	18	3	17	30	15	15	16
Number of Countable Individuals	444	355	873	1,318	570	703	2,709
Number of Polychaete Individuals	244	236	561	886	293	523	1,657
Number of Arthropod Individuals	117	6	58	293	52	39	67

Appendix Table III. Visual fish transect data taken on the dates shown below at the primary study site (100 m^2) at Johnston Atoll. The fish species are categorized first according to trophic status; in the body of the table are the number of individuals of each species observed in the study area.

	1975			1976	
	27 May	17 Aug.	14 Oct.	24 Apr.	25 Apr.
I. HERBIVORES					
Family Acanthuridae (Surgeonfishes)					
Acanthurus achilles	11	31	18	18	13
A. dussumieri		3	13	23	7
A. nigrofuscus	7	56	23	65	43
A. nigroris	27	26	27	18	10
A. olivaceus					2
A. triotegus sandvicensis		12	3	4	9
Ctenochaetus strigosus	37	45	43	51	55
Naso literatus		3	2	9	4
N. unicornis					1
Zebrasoma flavescens	3	12	1		1
Family Kyphosidae (Rudderfishes)					
Kyphosus cinerascens					1
Family Pomacentridae (Damselfishes)					
Abudefduf sordidus			1		
Family Scaridae (Parrotfishes)					
Scarus dubius	3	6	7	21	5
S. forsteri	2				
S. perspicillatus	1	1	2	3	4
S. sordidus	9	78	43	~215	~300
S. taeniurus				22	37
juvenile scarids	23	15		~60	
Calotomus spinidens		1	1	2	
TOTALS:					
Number of Individuals	123	289	184	511	492
Number of Species	10	13	13	13	15

Appendix Table III. (continued)

	1975			1976	
	27 May	17 Aug.	14 Oct.	24 Apr.	25 Apr.
II. OMNIVORES					
Family Balistidae (Triggerfishes)					
Melichthys niger	2	3	2	4	2
M. vidua				1	
Rhinecanthus rectangulus				1	
Family Chaetodontidae (Butterflyfishes)					
Chaetodon auriga	1	4		2	2
C. ephippium		2			
C. quadrimaculatus		1	1	1	2
Family Labridae (Wrasses)					
Gomphosus varius	3	8	2		2
Thalassoma lutescens	4	9	7	18	7
Stethojulis balteata		19	17	4	4
Family Monacanthidae					
Cantherines sandwichiensis		1			2
Family Zanclidae					
Zanclus canescens	2	1	1		2
TOTALS:					
Number of Individuals	12	47	30	31	23
Number of Species	5	9	6	7	8

Appendix Table III. (continued)

	1975			1976	
	27 May	17 Aug.	14 Oct.	24 Apr.	25 Apr.
III. CARNIVORES					
Family Aulostomidae (Trumputfishes)					
Aulostomus chinensis			1	1	1
Family Blennidae (Blennies)					
Exallias brevis				1	
Family Chaetodontidae (Butterflyfishes)					
Megaprotodon tricascialis	3		3	3	2
Family Cirrhitidae					
Cirrhitus pinnulatus				1	1
Paracirrhites arcatus			2		2
P. forsteri	1			4	
Family Carangidae (Jacks)					
Caranx melampygus			2	1	4
Family Fistulariidae (Cornetfishes)					
Fistularia petimba				1	
Family Labridae (Wrasses)					
Anampses cuvieri	2	4		2	1
A. rubrocaudatus	1	1			
Cheilinus rhodochrous	3	6	2	2	1
Coris gaimardi	1	3	3		2
C. venusta			1		
Labroides phthirophagus		1	1	1	1
Macropharyngogon geoffroyi	2	1			
Thalassoma duperryi	18	13	9	3	
Thalassoma umbrostigma	2	2	5	2	
T. purpureum	1	2	10	2	
Epibulus insidiator	3	2	4	3	
Family Lutjanidae (Snappers)					
Aphareus furcatus	1	2		1	
Family Mullidae (Goatfishes)					
Mulloidichthys flavolineatus				4	
Parupeneus bifasciatus				1	
P. chryserydros	1		2	1	
P. multifasciatus		4	3		1

Appendix Table III. (continued)

	1975			1976	
	27 May	17 Aug.	14 Oct.	24 Apr.	25 Apr.
III. CARNIVORES (continued)					
Family Pomacentridae (Damselfishes)					
Abudefduf imparipennis		3	2	3	2
Chromis hanui	3				
C. ovalis				1	2
Dascyllus albisella				3	3
Plectroglyphidodon johnstonianus				1	1
TOTALS:					
Number of Individuals	40	45	51	42	24
Number of Species	13	13	16	22	14

Appendix Table IV. Results of the first microcosm grazing experiment for benthic taxa encountered in samples collected on the ungrazed side after 91 days exposure. Each sample (scrape) is 100 cm^2 in surface area; numbers 1 and 5 were taken 10 cm below the water surface and 2 through 4, 20 cm below the surface.

	SCRAPE NUMBER									
	1		2		3		4		5	
GROUP	Number	Dry Weight	Number	Dry Weight	Number	Dry Weight	Number	Dry Weight	Number	Dry Weight
Phylum Chlrophyta										
Ulva lactuca		0.087		0.310				1.155		
Phylum Cnidaria										
Order Actinaria					1				1	0.341
Order Madreporaria										
Cyphastrea ocellina					7	0.010			2	0.004
Phylum Platyhelminthes										
Class Turbellaria			1				3	0.001	2	0.015
Phylum Mollusca										
Class Gastropoda										
Nerita picea			1	0.032						
Bulla adamsi (juv)			2	0.007						
Cypraea caputserpentis (juv)			1	1.001						
Class Bivalvia										
Isognomon californicum	4	0.113	6	0.769	1	0.200			8	0.291
Ostrea sandvichensis			6	4.053	11	3.365	4	2.043		
Anomia sp.	12	0.604	31	5.427	25	5.261	26	4.917	9	2.452

Appendix Table IV. (continued)

GROUP	SCRAPE NUMBER 1 Number	1 Dry Weight	2 Number	2 Dry Weight	3 Number	3 Dry Weight	4 Number	4 Dry Weight	5 Number	5 Dry Weight
Phylum Annelida										
Class Polychaeta										
Syllis (Syllis) gracilis	16		51		8		121		12	
Trypanosyllis zebra	4		8		4		2		2	
Branja oculata (?)	5		3						1	
Autolytinae sp.									1	
Syllid stolons	4		11		6		37		4	
Ceratonereis mirabilis	9		26		10		31		3	
Platynereis dumerilii	2		2		7		10		5	
Pseudonereis variegata			16							
Ophryotrocha sp. 1			1		3		4			
Dorvillea sp. 1							1		1	
Nereis (Neanthes) caudata					1					
Ophelina sp. 1			4				4			
Capitella capitata	1	0.122		0.177		0.335		0.368		0.148
Family Capitellidae sp. 1							1			
Branchiomma cingulata	1		2				1		1	
Family Sabellidae sp. 1							1			
Polydora websteri					1					
P. socialis					1					
Streblosoma sp.	1									
Hydroides dirampha	1				1		1		1	
H. elegans	1		2						2	
Hydroides sp.					1					
Family Cirratulidae sp. 1	152		667		269		2711	0.199	105	0.075
Pomatoleios kraussii							1			
Polychaete sp. 1	2									

Appendix Table IV. (continued)

GROUP	SCRAPE NUMBER 1 Number	1 Dry Weight	2 Number	2 Dry Weight	3 Number	3 Dry Weight	4 Number	4 Dry Weight	5 Number	5 Dry Weight
Phylum Arthropoda										
Subclass Cirripedia										
Balanus amphitrite	38	2.689	10	0.273	7	0.657	11	0.320	4	0.242
B. eburneus	3	0.071			9	0.257	4	0.388	5	0.522
Subclass Copepoda										
Copepod sp. 1	6		75		14		28		9	
sp. 2	3		55		18		72		5	
sp. 3	2		131		4		20		13	
sp. 4			67		35		113		6	
sp. 5			47		10		21		4	
sp. 6			45		7		32		2	
sp. 7		0.002	30	0.006		0.002	30	0.009		0.002
sp. 8			10				5			
sp. 9							56			
sp. 10							170			
Subclass Malacostraca										
Tanaidacea sp. 1			1		1		1			
Amphipoda sp. 1			5		1		9		3	
sp. 2			2		1		13			
sp. 3			1				6			
Decapoda										
Palaemon sp. 1 (juv)	1						3			
Shrimp sp. (juv)			7				2			
Crab megalops	1									
Epixanthus sp. 1							1	0.472		
Phylum Bryozoa									5	0.291
Schizoprella sp. 1										

Appendix Table IV. (continued)

GROUP	SCRAPE NUMBER 1 Number	1 Dry Weight	2 Number	2 Dry Weight	3 Number	3 Dry Weight	4 Number	4 Dry Weight	5 Number	5 Dry Weight
Phylum Chordata										
Sybphylum Urochordata										
Didemnum candidum		0.986		0.005		0.024		0.003		
Polyclinum sp. 1		0.109								0.049
Tunicata sp. 1 (colonial)		0.001		0.006		0.117		0.001		0.002
Misc. Organism Remains		0.438		0.403		0.464		0.981		
Total Number of Species	22		33		28		36		27	
Total Number of Individuals	269		1327		464		3558		216	
Total Dry Weight (g)	5.222		12.462		10.692		10.658		4.360	
Dry Weight (g/m^2)	522		1246		1069		1066		436	
Average Dry Wt. (g/m^2) = 867 g										

Appendix Table V. Results of the first microcosm grazing experiment for benthic taxa encountered in samples collected on the grazed side after 91 days exposure to 3 parrotfish approximately 10 g in weight (wet). Each sample (scrape) is 100 cm^2 in surface area; numbers 1 and 5 were taken 10 cm below the water surface and 2 through 4, 20 cm below the surface.

	SCRAPE NUMBER									
	1		2		3		4		5	
GROUP	Number	Dry Weight	Number	Dry Weight	Number	Dry Weight	Number	Dry Weight	Number	Dry Weight
Phylum Cyanophyta										
Family Oscillatoriaceae sp. 1			x	0.014	x		x		x	
sp. 2			x		x		x			
sp. 3							x		x	0.034
Phylum Mollusca										
Class Gastropods										
Family Vermetidae sp. 1 (juv)	1	0.027							1	
Class Bivalvia sp. 1 (juv)							1			
Phylum Annelida										
Class Polychaeta										
Pomatoleios kraussii					1	0.104		0.007		
Phylum Arthropoda										
Subclass Copepoda										
Copepod sp. 4					1					
sp. 5					1					
Phylum Chordata										
Subphylum Urochordata										
Ascidia sp. 1 (juv)					27		6			
Total Number of Species	1		2		6		5		3	
Total Number of Individuals	1		2		32		10		3	
Total Dry Weight (g)		0.027		0.014		0.104		0.007		0.034
Dry Weight (g/m^2)		2.7		1.4		10.4		0.7		3.4
Average Dry Weight g/m^2 = 3.7										

Appendix Table VI. Components of the benthic community, by number and dry weight biomass, developing in a 10 × 10 cm area on terracotta plates in a microcosm tank and subjected to no grazing by *Scarus* for a 36 day period. Four categories of exposure (refuge effect) are given by the presence of screen of different mesh sizes.

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Chlorophyta		0.003						
Ulva lactuca	x							
Phylum Protozoa		0.002		0.004		0.001		0.001
Class Rhizopodea								
Triloclina sp. 1	22		73		2		2	
Cymbaloporella sp. 1	1		9				1	
Phylum Cnidaria		0.004				0.002		0.002
O. Madreporaria								
Pocillopora damicornis	1				1		1	
Phylum Platyhelminthes		0.008		0.010				0.006
Class Turbellaria								
sp. 1	1		2				1	
sp. 2	1							
Phylum Nematoda	1	0.003	6	0.001		0.002		
Phylum Mollusca								
Class Gastropoda		0.003				0.010		0.016
micromollusca sp. 1			2					
sp. 2	1							
Hipponix pilosus					1			
Crepidula oculeata	1							
Family Vermetidae					1		1	
Nudibranch sp. 1							1	

Appendix Table VI. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Mollusca (cont.)								
Class Bivalvia		0.675		1.040		0.517		1.061
Anomia sp. 1	37		39		14		30	
Hiatella hawaiiensis							10	
Ostrea sandvichensis	21		10		5		6	
Isognomon costellatum			3		2		4	
I. californicum	6		11		3		3	
Mytilus cerebristriatus			1					
Phylum Annelida		0.013		0.054		0.242		0.566
Class Polychaeta								
Syllis (Typosyllis) variegata							7	
Syllis (Typosyllis) sp. 1			1					
Syllis armica			2					
Syllis sp. 1			1					
Tryanosyllis zebra	5		2		6		2	
Syllides sp. 1			1				1	
Ceratonereis mirabilis	94		69		25		33	
Eulalia sanguinea	2		1					
Syllidia armata			1					
Family Spionidae sp. 1			1					
Family Orbiniidae sp. 1			1					
Branchiomma nigromaculata			7		11			
Janua steueri	1				30		7	
Spirorbis sp. 1							1	
Hydroides sp. 1					1			
Phylum Arthropoda								
Class Crustacea								
Subclass Copepoda								
sp. 1			2		1			
sp. 2			1		1			
Subclass Cirripidia		2.047		0.890		1.381		0.893
Balanus trigonus	86		26		129		20	

Appendix Table VI. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Arthropoda (cont.)								
B. eburneus	6		3		4		1	
Subclass Malacostraca				0.001		0.051		0.060
O. Tanaidacea	1		3				1	
O. Amphipoda								
Gammaridea sp. 1			1		5		3	
sp. 2					8		2	
sp. 3							5	
Corophium baconi							1	
Caprellidea	1		2		1			
O. Decapoda								
Natantia								
Palaemon sp. 1			1					
Section Brachyura								
Pilumnus oahuensis							1	
Pilodius flavus					1			
xanthid sp. 1							1	
sp. 2					1			
Phylum Echinodermata				0.006				
Class Holothuroidea								
Opheodesoma spectabilis			1					
Phylum Chordata						0.092		0.314
Class Ascidiacea								
Didemnum candidum					3		7	
Didemnum sp. 1					2		5	
Botryloides sp. 1					1			
Ascidia sidneiensis							2	

Appendix Table VI. (continued)

	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Total Number of Species	20		30		25		29	
Total Number of Individuals	289		283		259		160	
Biomass (dry weight g/m^2)		276		201		230		292
Diversity (H')	1.86		2.31		1.96		2.66	

Appendix Table VII. Components of the benthic community, by number and dry weight biomass, developing in a 10 × 10 cm area on terracotta plates in a microcosm tank and subjected to variable grazing by a single *Scarus* during a 36 day period. Four categories of exposure (refuge effect) are given by the presence of screen of different mesh sizes.

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Protozoa				0.006		0.002		
Class Rhizopodia								
Triloclina sp. 1			22		1		2	
Phylum Porifera						0.003		
Class Calcarea					2			
Phylum Cnidaria		0.007		0.003		0.008	10	0.012
O. Madreporaria								
Pocillopora damicornis	8		4		7			
Phylum Platyhelminthes						0.0013		0.005
Class Turbellaria					3		2	
sp. 2								
Phylum Mollusca								
Class Gastropoda		0.002		0.008				0.004
micromollusca sp. 1							1	
sp. 2			1					
Family Vermetidae			1					
Class Bivalvia		0.115		1.210		0.831		1.946
Anomia sp. 1	84		37		33		61	
Hiatella hawaiiensis	2		1		6		12	
Ostrea sandvichensis	9		14		20		21	
Isognomon costellatum	3		2		4		5	
I. californicum	1						3	
Mytilus cerebristratus	1							

Appendix Table VII. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Annelida		0.030		0.055		0.330		0.209
Class Polychaeta								
Syllis (Typosyllis) variegata			3		4		6	
Tryanosyllis zebra							4	
Syllis sp. 1			3				2	
Family Syllidae sp. 4	2							
Exogoninae sp. 1	6						1	
Autolytinae sp. 1							1	
Ceratonereis mirabilis	8		59		100		55	
Platynereis dumerilli	13		5		3		7	
Eulalia sanguinea			1		1		1	
Polydora sp. 1					1			
Branchiomma nigromaculata	4		3		30		18	
Janua steueri					4			
Pileolaria militaris					1			
Phylum Arthropoda								
Class Crustacea				0.022		0.005		0.003
Subclass Copepoda								
sp. 1	46		1					
sp. 2	3		1					
sp. 3	1							
Subclass Cirripidia		0.146		0.229		0.036		0.401
Balanus trigonus	6		8		5		12	
B. amphitrite							1	
B. eburneus							1	
Subclass Malacostraca						0.245		
O. Amphipoda								
Gammaridea sp. 1					1		1	
Caprellidea								
O. Decapoda								
Natantia								
Palaemon sp. 1			2					

Appendix Table VII. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Arthropoda (cont.)								
Section Brachyura								
Pilumnus oahuensis					1			
Clibinarius zebra					1			
Phylum Bryzoa						0.002		0.002
Bryozoa sp. 1					1		3	
Phylum Chordata		0.019		0.020		0.005		0.027
Class Ascidiacea								
Didemnum candidum	1						1	
Ascidia sidneiensis	1		3		3		3	
Ascidia sp. 1					1		3	
Botryloides sp. 1			1		1		1	
Total Number of Species	16		21		26		27	
Total Number of Individuals	150		220		236		238	
Biomass (dry weight g/m^2)		32		155		148		261
Diversity (H')	1.73		2.19		2.08		2.43	

Appendix Table VIII. Components of the benthic community by number and dry weight biomass, developing in a 10 × 10 cm area on terracotta plates in a microcosm tank and subjected to variable grazing by two *Scarus* during a 36 day period. Four categories of exposure (refuge effect) are given by the presence of screen of different mesh sizes.

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Protozoa				0.003				0.003
Class Rhizopodea								
Triloclina sp. 1	3		6				4	
Cymbaloporella sp. 1	6						1	
Phylum Cnidaria		0.001		0.004		0.001		0.006
O. Madreporaria								
Pocillopora damicornis	2		2		2		3	
Phylum Platyhelminthes						0.004		0.011
Class Turbellaria								
sp. 1					1		1	
sp. 2							1	
sp. 3							1	
Phylum Mollusca								
Class Gastropoda				0.001		0.002		0.003
micromollusca sp. 1							1	
sp. 4							2	
Family Vermetidae							1	
Veliger								
Class Bivalvia		0.053		1.249		1.559		1.290
Anomia sp. 1	21		19		36		23	
Hiatella hawaiiensis			1		10		7	
Ostrea sandvichensis	6		6		11		10	
Isognomon costellatum			4		2		3	
I. californicum			3		4		5	

Appendix Table VIII. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Annelida		0.007		0.014		0.112		0.142
Class Polychaeta								
Syllis (Typosyllis) variegata					6		11	
Syllis sp. 1					4		3	
Tryanosyllis zebra			1				4	
Family Syllidae sp. 4	7							
Syllidia armata							1	
Exogoninae sp.	2							
Ceratonereis mirabilis			12		51		85	
Platynereis dumerilli			10		18		7	
Branchiomma nigromaculata			1		24		14	
Janua steueri					1		1	
Pileolaria pseudomilitaris					1		1	
Hydroides elegans							1	
Pomatoleios krausii							1	
Phylum Arthropoda								
Class Crustacea		0.004		0.003		0.005		0.004
Subclass Copepoda								
sp. 1	43		16		2		1	
sp. 2	3		5					
sp. 3			6					
sp. 4					1			
Subclass Cirripidia		0.722		0.690		0.633		1.142
Balanus trigonus	21		11		26		42	
B. amphitrite			2				1	
B. eburneus							1	
Subclass Malacostraca								0.004
O. Tanaidacea					1			
O. Isopoda					2			
O. Amphipoda								
Gammaridea sp. 1					4			
sp. 2					3		2	
sp. 3					1			

Appendix Table VIII. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Arthropoda (cont.)								
Caprellidea					2		1	
O. Decapoda								
Natantia								
Palaemon sp. 1							1	
Section Brachyura								
Pilodius flavus							1	
Phylum Bryzoa						0.003		0.005
Bugula californica							1	
Bryozoa sp. 1					3		2	
Phylum Chordata				0.007		0.170		0.136
Class Ascidiacea								
Didemnum candidum			2		2		2	
Ascidia sidneiensis					4		7	
Ascidia sp. 1					5		5	
Botryloides sp. 1			1		3		6	
Total Number of Species	13		19		29		39	
Total Number of Individuals	134		109		231		265	
Biomass (dry weight g/m^2)		79		197		249		275
Diversity (H')	2.08		2.56		2.62		2.59	

Appendix Table IX. Components of the benthic community by number and dry weight biomass developing in a 10 × 10 cm area on terracotta plates in a microcosm tank and subjected to variable grazing by three *Scarus* during a 36 day period. Four categories of exposure (refuge effect) are given by the presence of screen of different mesh sizes.

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Protozoa				0.006				
Class Rhizopodea								
Triloclina sp. 1	6		15					
Cymbaloporella sp. 1			1					
Phylum Porifera						0.003		
Class Demospongia					3		2	
Phylum Cnidaria				0.003		0.012		0.007
O. Madreporaria								
Pocillopora damicornis			3		13		8	
Phylum Platyhelminthes		0.004						
Class Turbellaria								
sp. 1								
sp. 2	3				1		2	
Phylum Nematoda							96	0.031
Phylum Mollusca				0.004				
Class Gastropoda								0.015
micromollusca sp. 1							1	
Hipponix pilosus							1	
Bulla adamsi								
Tethys bipes							1	
Class Bivalva		0.305		0.492		1.225		1.948
Anomia sp. 1	32		32		44		67	
Hiatella hawaiiensis			1		16		8	
Ostrea sandvichensis	6		3		17		19	

Appendix Table IX. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Mollusca (cont.)								
Isognomon costellatum			2		4		6	
I. californicum			1		1		1	
Phylum Annelida		0.007		0.027		0.317		0.207
Class Polychaeta								
Syllis (Typosyllis) variegata					9		3	
Syllis sp. 1	3		1		3			
Family Syllidae sp. 3	3							
sp. 4			8		6		3	
Trypanosyllis zebra	3				3		3	
Ceratonereis mirabilis	48		21		58		49	
Platynereis dumerilli	8		14		4		10	
Hydroides elegans					1		1	
Janua steueri					35		15	
Pileolaria pseudomilitaris							1	
Branchiomma nigromaculata			1		28		24	
Exogoninae sp.	3							
Family Dorvilleidae sp. 1					1			
Polydora sp. 1	1							
Phylum Arthropoda								
Class Crustacea		0.006		0.012		0.008		0.010
Subclass Copepoda								
sp. 1	24		52		1		4	
sp. 2	8				1		1	
sp. 3			18				3	
sp. 4	6		3					
sp. 5			6					
Subclass Cirripidia		3.868		0.954		2.076		1.120
Balanus trigonus	135		27		111		46	
B. amphitrite					3		1	
B. eburneus					3		1	

Appendix Table IX. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Arthropoda (cont.)								
Subclass Malacostraca						0.085		0.023
O. Tanaidacea			1				1	
O. Isopoda			1					
O. Amphipoda								
Gammaridea sp. 1					2			
sp. 4			1				5	
Caprellidea	11		4		24		33	
O. Decapoda								
Section Brachyura								
Pseudozius caystrus					1		1	
Phylum Bryozoa				0.001		0.005		0.002
Bugula californica			1					
Bryozoa sp. 1					3		6	
Phylum Chordata						0.233		0.248
Class Ascidiacea								
Didemnum candidum							5	
Ascidia sidneiensis					6		7	
Ascidia sp. 1					7		1	
Botryloides sp. 1					8		3	
Total Number of Species	18		26		30		36	
Total Number of Individuals	308		221		417		439	
Biomass (dry weight g/m^2)		419		150		397		361
Diversity (H')	1.98		2.48		2.60		2.65	

Appendix Table X. Components of the benthic community by number and dry weight biomass developing in a 10 × 10 cm area on terracotta plates in a microcosm tank and subjected to variable grazing by four *Scarus* during a 36 day period. Four categories of exposure (refuge effect) are given by the presence of screen of different mesh sizes.

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Protozoa				0.003		0.002		
Class Rhizopodea								
Triloclina sp. 1			1		3			
Cymbaloporella sp. 1					1			
Phylum Porifera						0.003		
Class Demospongia					2			
Phylum Cnidaria		0.003		0.020		0.002		0.015
O. Madreporaria								
Pocillopora damicornis	2		12		1		12	
Phylum Platyhelminthes				0.004		0.028		0.002
Class Turbellaria								
sp. 2			1		12		1	
Phylum Mollusca				0.003				0.008
Class Gastropoda								
micromollusca sp. 1			1		2		1	
Hipponix pilosus							1	
Family Vermetidae							1	
Class Bivalvia		0.213		0.792		1.434		1.018
Anomia sp. 1	2		36		39		36	
Hiatella hawaiiensis					8		7	
Ostrea sandvichensis			7		17		12	
Isognomon costellatum			2		1		1	
I. californicum			1				2	
Mytilus cerebristriatus	1		1					

Appendix Table X. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Annelida		0.005		0.029		0.484		0.139
Class Polychaeta								
Syllis (Typosyllis) variegata	1		1		3			
Syllis sp. 1					1			
Exogininae sp.					1			
Trypanosyllis zebra			12					
Family Syllidae sp. 1			2		1			
Eulalia sanguinea					3			
Syllides armata					1			
Polydora sp. 1					1			
Ceratonereis mirabilis	2		49		124		51	
Platynereis dumerilli			10		15		26	
Branchiomma nigromaculata			1		36		14	
Janua steueri							1	
Phylum Arthropoda								
Class Crustacea				0.004		0.003		0.002
Subclass Copepoda								
sp. 1	2		6		3		3	
Subclass Cirripidia		0.111		0.591		0.680		1.437
Balnus trigonus	7		9		59		56	
B. amphitrite					1		3	
B. eburneus			1					
Subclass Malacostraca								
O. Amphipoda								
Gammaridea sp. 1			1		1			
sp. 2							4	
Caprellidea					3		1	
O. Decapoda						0.001		
Section Brachyura								
Pilodius flavus					1			
Phylum Bryozoa								0.009
Bugula californica							1	
Bryozoa sp. 1					2		1	

Appendix Table X. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Chordata				0.011		0.341		0.067
Class Ascidiacea								
Didemnum candidum	1		2		5			
Ascidia sidneiensis	2		11		5			
Ascidia sp. 1			3		4			
Botryloides sp. 1			3		1			
colonial tunicate sp. 1			1					
Total Number of Species	6		20		31		28	
Total Number of Individuals	16		145		370		255	
Biomass (dry weight g/m^2)		33		146		298		270
Diversity (H')	1.57		2.07		2.33		2.45	

Appendix Table XI. Components of the benthic community by number and dry weight biomass developing in a 10 × 10 cm area on terracotta plates in a microcosm tank and subjected to variable grazing by five *Scarus* during a 36 day period. Four categories of exposure (refuge effect) are given by the presence of screen of different mesh sizes.

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Protozoa				0.001				
Class Rhizopodea								
Triloclina sp. 1			1		1			
Cymbaloporella sp. 1			1					
Phylum Porifera						0.009		0.005
Class Calcarea					9		6	
Class Demospongia					1			
Phylum Cnidaria						0.005		0.011
O. Madreporaria								
Pocillopora damicornis					6		7	
Phylum Platyhelminthes				0.003		0.002		0.004
Class Turbellaria								
sp. 1							1	
sp. 2			1		1		3	
Phylum Nematoda					6	0.001	2	
Phylum Mollusca								
Class Gastropoda						0.003		
micromollusca sp. 3					1			
Family Vermetidae					1			
Class Bivalvia				0.673		1.433		1.456
Anomia sp. 1			23		38		32	
Hiatella hawaiiensis					5		11	
Ostrea sandvichensis					15		11	
Isognomon costellatum							4	

Appendix Table XI. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
I. californicum			1				1	
Mytilus cerebristriatus							1	
Phylum Annelida		0.006		0.013		0.154		0.082
Class Polychaeta								
Syllis (Typosyllis) variegata					1		4	
Syllis sp. 1							4	
Trypanosyllis zebra					4		1	
Exogoninae sp.							1	
Syllides sp. 1					5		3	
Family Syllidae sp. 1							2	
sp. 2							3	
Eulalia sanguinea							1	
Ceratonereis mirabilis	5		12		74		56	
Platynereis dumerilii			23		11		21	
Branchiomma nigromaculata					8		5	
Hydroides elegans					1		1	
Pileolaria militaris					2		1	
Janua steueri					2		1	
Phylum Arthropoda								
Class Crustacea								
Subclass Copepoda								
sp. 1							64	
sp. 2					1		18	
sp. 3			2		1		5	
sp. 5							1	
Subclass Cirripidia		0.504		0.578		0.622		2.238
Balanus trigonus	11		21		42		135	
B. eburneus	2				3		1	
Subclass Malacostraca				0.045		0.072		0.014
O. Tanaidacea							4	
O. Isopoda					1			

Appendix Table XI. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Arthropoda (cont.)								
O. Amphipoda								
Gammaridea sp. 1					1			
sp. 2			2		3			
sp. 3							2	
sp. 4			6		3		1	
Caprellidea					3		6	
O. Decapoda								
Natantia								
Palaemon sp. 1					1			
Section Brachyura								
Pilodius flavus					1			
Lophozozymus dodone			1		1			
Phylum Bryozoa								0.005
Bugula californica							1	
Bryozoa sp. 1							2	
Phylum Chordata						0.088		0.045
Class Ascidiacea								
Didemnum candidum							1	
Didemnum sp. 1							1	
Ascidia sidneiensis					7		1	
Ascidia sp. 1							1	
Botryloides sp. 1					1		2	
Total Number of Species	4		13		32		42	
Total Number of Individuals	20		94		259		429	
Biomass (dry weight g/m^2)		51		131		239		386
Diversity (H')	1.14		1.88		2.51		2.51	

Appendix Table XII. Components of the benthic community by number and dry weight biomass developing in a 10 × 10 cm area on terracotta plates in a microcosm tank and subjected to variable grazing by six *Scarus* during a 36 day period. Four categories of exposure (refuge effect) are given by the presence of screen of different mesh sizes.

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Protozoa				0.002				
Class Rhizopodea								
Triloclina sp. 1			3				1	
Phylum Porifera						0.004		
Class Demospongia					2			
Phylum Cnidaria				0.002		0.025		0.028
O. Actinaria								0.003
Radianthus cookei							1	
O. Madreporaria								
Pocillopora damicornis			3		18		17	
Phylum Platyhelminthes		0.003				0.003		0.002
Class Turbellaria								
sp. 1					1			
sp. 2	2				4		1	
Phylum Nematoda			3					
Phylum Mollusca								
Class Gastropoda						0.001		0.002
micromollusca sp. 1					1		1	
Class Bivalvia		0.034		0.592		1.919		1.508
Anomia sp. 1	12		19		56		37	
Hiatella hawaiiensis			2		3		5	
Ostrea sandvichensis			9		18		7	
Isognomon costellatum	1							
Lithophaga sp.					1			

Appendix Table XII. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Annelida		0.001		0.013		0.101		0.148
Class Polychaeta								
Syllis (Typosyllis) variegata					2		2	
Syllis sp. 1	1				2			
Family Syllidae sp. 4			2					
Typosyllis sp. 1					1		1	
Tryanosyllis zebra					2			
Exogoninae sp.							1	
Ceratonereis mirabilis	2		6		109		77	
Platynereis dumerilii	1		13		17		7	
Janua steueri					19		2	
Serpula vermicularis							1	
Pomatoleios kraussii					1		1	
Pileolaria militaris					1			
Branchiomma nigromaculata	1				11		20	
Phylum Arthropoda								
Class Crustacea						0.002		0.005
Subclass Copepoda								
sp. 1					9		1	
Subclass Cirripidia		1.122		0.501		0.711		0.931
Balanus trigonus	34		14		35		25	
B. amphitrite			2		1		1	
B. eburneus							1	
Subclass Malacostraca								
O. Tanaidacea							1	
O. Amphipoda								
Gammaridea sp. 1					1			
sp. 2							1	
sp. 5							1	
O. Decapoda								
Natantia								
Palaemon sp. 1							1	

Appendix Table XII. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Echinodermata						0.011		
Class Ophiuroidea								
Ophiactis savignyi					1			
Phylum Chordata						0.115		0.131
Class Ascideacea								
Ascidia sidneiensis					2		3	
Ascidia sp. 1					4		1	
Ascidia nigra					1		1	
Botryloides sp. 1					4		1	
Total Number of Species	8		11		28		30	
Total Number of Individuals	54		76		327		221	
Biomass (dry weight g/m^2)		116		111		289		276
Diversity (H')	1.17		2.08		2.28		2.24	

Appendix Table XIII. Components of the benthic community by number and dry weight biomass developing in a 10 × 10 cm area on terracotta plates in a microcosm tank and subjected to variable grazing by seven *Scarus* during a 36 day period. Four categories of exposure (refuge effect) are given by the presence of screen of different mesh sizes.

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Protozoa						0.003		
Class Rhizopodea								
Triloclina sp. 1					5			
Cymbaloporella sp. 1					1			
Phylum Porifera						0.003		
Class Demospongia					1			
Phylum Cnidaria				0.016		0.015		0.006
O. Madreporaria								
Pocillopora damicornis			14		21		5	
Phylum Platyhelminthes						0.005		0.009
Class Turbellaria								
sp. 1							1	
sp. 2					2		2	
Phylum Mollusca								
Class Gastropoda						0.007		
micromollusca sp. 1					4			
Hipponix pilosus					1			
Family Vermetidae					1			
Class Bivalvia		0.177		0.513		1.065		1.246
Anomia sp. 1			24		62		18	
Hiatella hawaiiensis					9		7	
Ostrea sandvichensis			1		16		3	
Isognomon costellatum	1				2		1	
I. costellatum	1						3	

Appendix Table XIII. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Annelida				0.014		0.115		0.081
Class Polychaeta								
Syllis (Typosyllis) variegata					2		3	
Syllis sp. 2					2		1	
Family Syllidae sp. 4					7		4	
Exogoninae sp.					1		1	
Trypanosyllis zebra					3		2	
Eulalia sanguinea							1	
Ceratonereis mirabilis					71		55	
Platynereis dumerilii					36		12	
Branchiomma nigromaculata					11		6	
Janua steueri					6		1	
Hydroides elegans							2	
Pileolaria militaris					1		1	
Phylum Arthropoda				0.004		0.004		0.005
Class Crustacea								
Subclass Copepoda								
sp. 1			5		2		2	
sp. 3					1			
sp. 6					1			
Subclass Cirripidia				0.637		0.832		2.658
Balanus trigonus	1		13		47		59	
B. amphitrite			2		3		4	
B. eburneus			1				3	
Subclass Malacostraca								
O. Tanaidacea	1		3				1	
O. Amphipoda								
Caprellidea							2	
Class Insects								
Pynogonida sp. 1					1			

Appendix Table XIII. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Bryozoa						0.007		0.005
Bryozoa sp. 1					2		4	
Phylum Chordata						0.018		0.017
Class Ascidiacea								
Didemnum candidum					1		3	
Ascidia sidneiensis					1		2	
Ascidia sp. 1					4		2	
Botryloides sp. 1							2	
Total Number of Species	6		12		32		31	
Total Number of Individuals	7		96		328		213	
Biomass (dry weight g/m^2)		18		118		207		403
Diversity (H')	1.75		2.03		2.50		2.45	

Appendix Table XIV. Components of the benthic community by number and dry weight biomass developing in a 10 × 10 cm area on terracotta plates in a microcosm tank and subjected to variable grazing by eight *Scarus* during a 36 day period. Four categories of exposure (refuge effect) are given by the presence of screen of different mesh sizes.

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Cnidaria				0.008		0.026		0.033
O. Madreporaria								
Pocillopora damicornis			7		16		23	
Phylum Platyhelminthes						0.006		0.011
Class Turbellaria								
sp. 1					1		1	
sp. 2					3		4	
Phylum Mollusca								0.005
Class Gastropoda						0.052		
Hipponix pilosus					3		1	
Family Vermetidae							1	
Class Bivalvia		0.011		0.153		1.759		1.811
Anomia sp. 1	2		14		36		24	
Hiatella hawaiiensis			1		13		9	
Ostrea sandvichensis			2		16		14	
Isognomon costellatum					12		3	
I. californicum					3		1	
Phylum Annelida		0.005		0.006		0.050		0.073
Class Polychaeta								
Syllis (Typosyllis) variegata					3		3	
Syllis sp. 1			1		3			
Tryanosyllis zebra							4	
Exogoninae sp.					1		1	
Family Syllidae sp. 1					2		1	
Autolytinae sp.							4	
Platynereis dumerilii			2		17		8	
Ceratonereis mirabilis	2		4		39		33	

Appendix Table XIV. (continued)

TAXONOMIC GROUP	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Phylum Annelida (cont.)								
Eulalia sanguinea					1		1	
Branchiomma nigromaculata			1		9		15	
Polydora sp. 1							1	
Pomatoleios kraussii							1	
Serpula vermicularis					1			
Pileolaria militaris	1				5			
Janua steueri					27			
Polychaete sp. 1							1	
Phylum Arthropoda								
Class Crustacea								
Subclass Copepoda								
sp. 1	3		7		3		1	
Subclass Cirripidia		1.377		0.749		1.767		3.410
Balanus trigonus	35		21		86		101	
B. amphitrite							1	
B. eburneus			2		1		1	
Subclass Malacostraca		0.004		0.005		0.002		0.003
O. Tanaidacea							1	
O. Isopoda					1		1	
O. Amphipoda								
Gammaridea sp. 3					1			
Caprellidea	2						2	
O. Decapoda								
Section Brachyura								
Family Xanthidae								
sp. 1							1	
megalops					1			
Phylum Chordata						0.060		0.110
Ascidia sidneiensis					7		3	
Ascidia sp. 1							1	
Botryloides sp. 1					4		3	

Appendix Table XIV. (continued)

	EXPOSED		FINE MESH		MEDIUM MESH		COARSE MESH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Total Number of Species	6		11		28		34	
Total Number of Individuals	45		62		315		273	
Biomass (dry weight g/m^2)		140		92		372		546
Diversity (H')	0.96		1.90		2.54		2.39	

Appendix Table XV. Number, weight and classification of fish collected after rotenone treatment from the Kaneohe Bay, Oahu experimental reef by Wass in 1966 and Brock in 1977. Classification is based upon feeding habits as reported in the literature or by stomach analysis. The classifications are: C = carnivore; P = plantivore; CP = coral polyp or mucous feeder; O = omnivore; H = herbivore; D = detritivore; and ?, questionable.

FAMILY AND SPECIES	WASS 1966		BROCK 1977		Feeding Category
	Number	Weight (g)	Number	Weight (g)	
Family Dussumieriidae					
Etrumeus micropus			8	792	P
Family Synodontidae					
Saurida gracilis			23	1,657	C
Synodus variegatus			1	47	C
S. dermatogenys	49	2,014			C ?
Family Muraenidae					
Uropterygius tigrinus	5	1,702	2	910	C
U. inornatus	3	32			C ?
U. fuscoguttatus	8	176	4	103	C ?
U. supraforatus	1	13			C
Anarchias cantonensis	1	24			C
Echidna zebra	20	10,512	6	4,178	C
E. polyzona			1	56	C ?
Gymnothorax eurostus	11	2,008	19	2,223	C
G. steindachneri	1	9	1	96	C
G. flavimarginatus			3	252	C
G. javanicus			1	1,912	C
G. meleagris			1	257	C
G. undulatus	66	9,700	164	7,631	C
G. hilonis (probably *G. pictus*)	3	97			C
Anarchias leucurus			7	107	C ?
G. gracilicaudus			1	39	C
G. buroensis			1	38	C
Gymnothorax sp.			1	5	C
Family Congridae					
Conger cinereus	31	2,267	8	400	C
C. oligoporus	15	186			C
Family Belonidae					
Strongylura gigantea	1	24			C
Family Aulostomidae					
Aulostomus chinensis	39	936	24	1,142	C
Family Fistulariidae					
Fistularia petimba	7	141			C
Family Syngnathidae					
Doryrhamphus melanopleura	3	3	2	1	P

Appendix Table XV. (continued)

FAMILY AND SPECIES	WASS 1966 Number	WASS 1966 Weight (g)	BROCK 1977 Number	BROCK 1977 Weight (g)	Feeding Category
Family Holocentridae					
Flammeo sammara	15	498			C
Adioryx lacteoguttatus	13	232	2 2	20	C
A. diadema	40	1,214	3 3	180	C
Plectrypops lima	3	327			C
Myripristes amaenus amaenus	34	896			P
Family Bothidae					
Bothus mancus			1 1	35	C
Family Pleuronectidae					
Samariscus triocellatus	2	5	2 2	22	C ?
Family Serranidae					
Ypsigramma sp.	1	14			
Family Pseudochromidae					
Pseudogramma polyacantha	16	232			C
Family Priacanthidae					
Priacanthus cruentatus	24	574	7 7	368	P
Family Apogonidae					
Foa brachygramma	356	882	1,090	2,066	
Apogon erythrinus			3	7	C
A. snyderi	212	5,919	123	3,016	C
A. menesemus	12	138			P
A. maculiferus	3	18			
Family Carangidae					
Caranx melampygus			11	917	C
Family Mullidae					
Mulloidichthys flavolineatus	36	3,067	12	2,002	C
M. vanicolensis			9	633	C
Parupeneus porphyreus			2	192	C
P. multifasciatus	4	392	2	39	C
Family Chaetodontidae					
Chaetodon fremblii	1	12			C
C. auriga	12	613	5	208	C
C. lunula	15	818			C
C. trifasciatus	1	35			CP
C. ornatissimus			1	10	CP
C. miliarus	476	16,756	421	18,063	P
Heniochus acuminatus			1	49	

Appendix Table XV. (continued)

FAMILY AND SPECIES	WASS 1966 Number	WASS 1966 Weight (g)	BROCK 1977 Number	BROCK 1977 Weight (g)	Feeding Category
Family Pomacentridae					
Dascyllus albisella	57	1,340	99	3,708	P
Abudefduf abdominalis	1,142	97,004	666	50,916	P
Chromis hanui			2	24	P
C. ovalis	6	67	7	139	P
Plectroglyphidodon johnstonianus	5	62	1	10	C
Eupomacentrus fasciolatus	52	1,745	44	1,770	O
Family Labridae					
Bodianus bilunulatus	5	38	5	180	C
Cheilinus rhodochrous	19	515	4	85	C
C. bimaculatus	11	176			C ?
Labroides phthirophagus	2	13			C
Pseudocheilinus evanidus	1	10			C ?
P. octotaenia	2	45			C
Thalassoma duperreyi	146	3,120	67	2,845	C
T. ballieui	2	58			C ?
Gomphosus varius	27	660	25	748	C
Stethojulius balteata	4	80	6	85	C
Macropharyngodon geoffroyi			3	61	C
Family Scaridae					
Scarus dubius	45	981			H
S. perspicillatus	68	3,396	19	2,861	H
S. sordidus	386	4,514	142	3,246	H
Scarus taeniurus			40	1,928	H
Scarus spp. (juveniles)			344	2,648	H
Family Zanclidae					
Zanclus canescens	58	1,917	3	275	C
Family Acanthuridae					
Acanthurus nigrofuscus	1	62	2	22	H
A. triostegus sandvicensis	12	422	7	104	H
A. dussumieri	1	179			H
A. xanthopterus			4	255	H
Ctenochaetus strigosus	10	686	15	710	D
Zebrasoma flavescens	4	141	54	2,856	H
Z. veliferum	1	64	5	938	H
Naso brevirostris	8	1,712			H
N. unicornis			1	48	H
Family Eleotridae					
Asterropteryx semipunctatus	1,016	384	988	511	D ?
Family Gobiidae					
Bathygobius cotticeps			6	8	
B. fuscus			5	2	C
Gnatholepis sp.			7	4	
Gobiidae sp. A			4	1	
sp. B			1	0.2	

Appendix Table XV. (continued)

FAMILY AND SPECIES	WASS 1966 Number	WASS 1966 Weight (g)	BROCK 1977 Number	BROCK 1977 Weight (g)	Feeding Category
Family Blennidae					
Cirripectus obscurus	4	46			?
Cirripectus variolosus			2	16	H
Istiblennius zebra			4	1	D
Family Brotulidae					
Brotula multibarbata	9	501	4	1,525	C
Microbrotula rubra		2			C ?
Family Scorpaenidae					
Taenianotus triacanthus	4	49	11	326	C
Dendrochirus brachypterus	15	185	15	1,061	C
Scorpaenopsis gibbosa	6	367	3	148	C
S. cacopsis			2	47	C
Scorpaena coniorta	6	43			C
Family Monacanthidae					
Pervagor spilosoma	25	227	14	349	O
Catherhines dumerili	2	8			O
C. verecundus (?)	2	49			
Family Ostraciontidae					
Ostracion meleagris	1	5	1	9	C
Family Canthigasteridae					
Canthigaster jactator	45	316	15	128	C
Family Diodontidae					
Diodon hystrix			3	7,112	C
D. holocanthus			1	401	C
Family Antennariidae					
Antennarius drombus			1	14	C
Antennarius moluccensis			1	27	C
Total Number of Species	76		81		
Total Number of Individuals	4,755		4,626		
Total Wet Weight	27	184 kg	139 kg		
Total Number of Families			29		
Shannon-Weaver H'	2.65		2.48		

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